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A NEW COMBINATION IN *PANICUM* (POACEAE) SUBGENUS
DICHANTHELIUM

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ABSTRACT

The new combination *Panicum sphaerocarpon* Elliott var. *isophyllum* (Scribner) R. Angelo is proposed.

KEY WORDS: *Panicum*, Poaceae, *Dichanthelium*.

In Gould & Clark (1978) the taxon that was generally known as *Panicum polyanthes* J.A. Schultes was treated as a variety under the name *Dichanthelium sphaerocarpon* (Elliott) Gould var. *isophyllum* (Scribner) Gould & Clark. According to Zuloaga (1987) and Lelong (1984) there is insufficient evidence at present to warrant elevating subgenus *Dichanthelium* to the generic level. If *Panicum polyanthes* is still to be considered as a variety of *Panicum sphaerocarpon*, then a new combination will be required. The new combination *Panicum sphaerocarpon* Elliott var. *polyanthes* (Schultes) A.S. Sherif was proposed (Sherif 1983). However, under Article 60 of the *International Code of Botanical Nomenclature* (1988), a name does not have priority outside of its own rank. According to Gould & Clark (1978), "The name *isophyllum* Scribner is the earliest varietal name to be applied to this taxon and must be retained even though the species basionym, *microcarpon*, is illegitimate." In light of this the correct new combination should be:

Panicum sphaerocarpon Elliott var. *isophyllum* (Scribner) R. Angelo, *comb. nov.* BASIONYM: *Panicum microcarpon* Muhlenberg var. *isophyllum* Scribner, Bulletin of the Agricultural Experiment Station of the University of Tennessee. 7:51. Figure 54. 1894. *Dichanthelium sphaerocarpon* Elliott var. *isophyllum* (Scribner) Gould & Clark, Ann. Missouri Bot. Gard. 65:1105. 1978. TYPE: UNITED STATES. Tennessee: Blount County, Alleghany Springs, E.E. Gayle, August 1890 (HOLOTYPE: US, Sheet #743578, not seen).

Panicum multiflorum Elliott, not Poiret, *Sketch Bot. S. Carolina*. 1:122. 1816. TYPE: UNITED STATES. South Carolina or Georgia: "Hab. in umbrosis. Flor. Mai. June" (HOLOTYPE: CHARL, not seen, photo in GH).

Panicum microcarpon Muhlenberg, not Muhlenberg *ex* Elliott, *Descr. Gram.* 111. 1817. TYPE: UNITED STATES. "40, c Jul. 12. e Cherokee." (HOLOTYPE: PH, not seen).

Panicum polyanthes J.A. Schultes, *Mantissa* 2:257. 1824. *Dichanthe-
lium sphaerocarpon* Elliott var. *polyanthes* (J.A. Schultes) Gould,
Brittonia 26:60. 1974. *Panicum sphaerocarpon* Elliott var. *polyan-
thes* (J.A. Schultes) A.S. Sherif, *Sida* 10:191. 1983. *Dichanthe-
lium polyanthes* (J.A. Schultes) Mohlenbrock, *Erigenia* 6:26. 1985.
TYPE: Based upon *P. multiflorum* Elliott (December 1816), not
Poiret (June 1816).

Panicum firmandum Steudel, *Syn. Pl. Glumac.* 1:418. 1855. TYPE:
UNITED STATES. North Carolina: M.A. Curtis (HOLOTYPE:
P, not seen).

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I thank Dr. Elizabeth A. Shaw and Dr. David E. Boufford for their assistance and advice. I thank Deborah Bell for assisting in the location of a type specimen.

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lium* (Poaceae) in the United States and Canada. *Ann. Missouri Bot. Gard.* 65:1088-1132.
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lium* (Poaceae) of the southeastern United States. *Brittonia* 36:262-273.
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NOMENCLATURAL NOTES FOR THE NORTH AMERICAN FLORA. VII

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ABSTRACT

The authorship of the following names is discussed: *Horkelia fusca* Lindl. var. *parviflora* (Nutt. ex Torr. & Gray) Wawra, *Lotus purshianus* Clements & Clements, *Madia exigua* (Smith) A. Gray, *Sagittaria latifolia* Willd. var. *obtusata* (Engelm.) Wiegand, *Sagittaria longiloba* Engelm. ex J.G. Sm., and *Thunbergia grandiflora* Roxb. The parenthetical scientific names for poison oak (*Toxicodendron pubescens* P. Mill.), for Spanish clover (*Lotus unifoliolatus* [Hook.] Benth.), and for staghorn sumac (*Rhus hirta* [L.] Sudworth) are viewed to be correct. Three new combinations are proposed: *Chamaecrista nictitans* (L.) Moench var. *patellaria* (DC. ex Colladon) Kartesz & Gandhi; *Lotus unifoliolatus* (Hook.) Benth. var. *helleri* (Britt.) Kartesz & Gandhi; and *Ruellia caroliniensis* (Walt.) Steud. var. *cinerascens* (Fern.) Kartesz & Gandhi.

KEY WORDS: Floristics, nomenclature, Acanthaceae, Alismataceae, Anacardiaceae, Asteraceae, Fabaceae, Rosaceae, Sparganiaceae, *Chamaecrista*, *Horkelia*, *Lotus*, *Madia*, *Rhus*, *Ruellia*, *Sagittaria*, *Thunbergia*, and *Toxicodendron*.

INTRODUCTION

Continuing with the "NOMENCLATURAL NOTES FOR THE NORTH AMERICAN FLORA" (Kartesz & Gandhi 1989, 1990a, 1990b, 1990c, 1991a, 1991b), a seventh note in the series is presented here towards advancing our understanding of North American plant names.

ACANTHACEAE

Ruellia caroliniensis var. *cinerascens*

Under the binomial *Ruellia ciliosa* Pursh, Fernald described var. *cinerascens*. Since we treat *R. ciliosa* as a synonym of *R. caroliniensis* (Walt.) Steud., but still recognize Fernald's variety, the following new combination is proposed.

***Ruellia caroliniensis* (Walt.) Steud. var. *cinerascens* (Fern.) Kartesz & Gandhi, comb. nov.** BASIONYM: *Ruellia ciliosa* Pursh var. *cinerascens* Fern., *Rhodora* 47:48. 1945. TYPE: U.S.A. Florida: Walton Co., Crestview, 22 Jul 1899, *Curtis* 6489 (US).

Thunbergia grandiflora

Thunbergia grandiflora, a native of India, has become naturalized in Florida (pers. comm. from Dr. R.C. Wunderlin). The authorship of *T. grandiflora* has been attributed to "Roxb." (Jackson 1895; Wasshausen in Nicolson 1991), or to "(Roxb. ex Rottl.) Roxb." (Mathew, *Fl. Carnatic*, Tamil Nadu, vol. 3. 1983, *fide* Nicolson (US), pers. comm.; Barker 1986), or to "(Roxb. ex Rottl.) Lodd." (Howard 1989). Mathew, Barker, and Howard believed that this species was based on *Flemingia grandiflora* Roxb. ex Rottl., the type species for the genus *Flemingia* Roxb. ex Rottl. According to the ICBN (Greuter *et al.* 1988:219), the legume genus name *Flemingia* Roxb. ex Ait. f. (*Hort. Kew.*, ed. 2, 4:349. 1812) has been conserved over the homonym *Flemingia* Roxb. ex Rottler (Ges. Naturf. Freunde Berlin Neue Schriften 4:202. 1803). Furthermore, the ICBN indicated that *F. grandiflora* is an illegitimate name. In the protologue of *F. grandiflora*, we found the name *T. fragrans* Roxb., cited "as a synonym" in a footnote, which infers that *F. grandiflora* was a renaming of *T. fragrans*; i.e., the name *F. grandiflora* is superfluous and illegitimate. However, Dr. Nicolson informed us that footnotes in Rottler's article were not by Rottler, but rather by Willdenow (editor of Rottler's article). Hence, Nicolson concluded that the name *F. grandiflora* is legitimate and that ICBN erred in its treatment of Rottler's binomial. With this established, we discuss the authorship of the binomial *T. grandiflora*.

Roxburgh's 1814 work (*Hort. Beng.*), in which the binomial *Thunbergia grandiflora* was proposed, does not contain valid descriptions. For *T. grandiflora*, Roxburgh did not refer to Rottler's published description of *F. grandiflora*; hence, the binomial *T. grandiflora* was invalid. Loddiges (*Bot. Cab.*, vol. 4(3): t. 324. Jan 1820) independently used the name *T. grandiflora* and provided an illustration and generalized remarks. Except for his comment that *T. grandiflora* was odorless, Loddiges' protologue did not provide an illustration with analysis and did not meet the requirements of ICBN Art. 44.1. He neither referred to Roxburgh nor cited any other reference. Since Loddiges stated that the plant was native to India, it is possible that he was aware of Roxburgh's

1814 usage of the name, but this speculation can not be verified. Subsequently, Roxburgh, again without referencing a botanical work, provided a description (in Ker-Gawler, Bot. Reg. 6: t. 495. Nov 1820) and thus validated the name.

Although Wasshausen (in Nicolson 1991:18) attributed the name *T. grandiflora* to Roxburgh, his treatment was followed by Nicolson's (editor and chief author of the publication) remarks that the nomenclature of this binomial remains unsettled. Until or unless additional nomenclatural evidence can be provided, we are compelled to accept Roxburgh alone as the author of the binomial dating from Nov 1820.

Thunbergia grandiflora Roxb. [Hort. Beng. 45. 1814, nom. nud.] in Ker-Gawler, Bot. Reg. 6: t. 495. Nov 1820. TYPE: Bot. Reg. 6: t. 495.

Flemingia grandiflora Roxb. ex Rottl., Ges. Naturf. Freunde Berlin Neue Schriften 4:202. 1803. TYPE: INDIA. Tamil Nadu, Madras, Marmelon(g), 28 Nov 1799, Berry s.n. (not traced; fide Nicolson).

ALISMATACEAE

Sagittaria latifolia var. *obtusata*

For his new varietal combination *Sagittaria latifolia* Willd. var. *obtusata*, Wiegand gave a direct and full reference to *S. obtusa* Muhl. ex Willd. and also cited a reference to *S. variabilis* Engelm. var. *obtusata* Engelm. in A. Gray (1856) as a synonym. Engelmann, who provided the treatment for the suborder Alismaceae (including *Alisma*, *Echinodorus*, and *Sagittaria*) in the second edition of Gray's *Manual* (fide Gray's preface; p. xii), also based his variety on *S. obtusa*.

Unfortunately, *Sagittaria obtusa* Muhl. ex Willd. is a later homonym of *S. obtusa* Thunb. Although the name *S. obtusa* Thunb. is superfluous, and thus illegitimate (Thunberg cited *S. obtusifolia* L. as a synonym), *S. obtusa* Muhl. ex Willd. must still be rejected as a later homonym (ICBN Art. 64.1). Therefore, "Muhl. ex Willd." must not be cited as a parenthetical author for either *S. latifolia* var. *obtusata* or for *S. variabilis* var. *obtusata*. Furthermore, Engelmann's new combination *S. variabilis* var. *obtusata* must be treated as a *nomen novum*, with its priority from 1856 (ICBN Art. 72.2, Note 1), and Engelmann must be placed as the parenthetical author for the name *S. latifolia* var. *obtusata*.

Sagittaria latifolia Willd. var. *obtusata* (Engelm.) Wiegand, Rhodora 27:186. 1925. BASIONYM: *Sagittaria variabilis* Engelm. var. *obtusata* Engelm. in A. Gray, *Man. Bot.*, ed. 2. 439. 1856. *Sagittaria obtusa* Muhl. ex Willd., *Sp. Pl.* 4:409. 1805, non Thunb., 1784. TYPE: U.S.A. Muhlenberg s.n. (PH; fiche!).

Sagittaria longiloba

The name *Sagittaria longiloba* has been generally attributed to Engelm. *ex* Torrey (Smith 1895; Bogin 1955; Soil Conservation Service 1982) or to Engelmann (Kaul 1986). Torrey (1859:212), in a footnote, indicated that he had a *Sagittaria* specimen (sent by Bigelow) and considered it to be the same as "*S. longiloba* Engelm." According to Torrey, Engelmann had provisionally proposed (in manuscript) the name *S. longiloba* for a west Texas *Sagittaria* and regarded *S. longiloba* to be closely related to *S. simplex* Torr. Although Torrey briefly described *S. longiloba* ("The leaves, however, are sagittate, with very long, narrow, and widely diverging lobes, a state in which we have never seen *S. simplex*"), he remarked that these characters were insufficient for separating it from *S. simplex*. Since Torrey did not accept the name *S. longiloba*, he did not validly publish it, and the name must not be attributed to him (ICBN Art. 34.1a). Subsequently, Smith (1895) accepted the name *S. longiloba*, attributed it to Engelmann *ex* Torrey, and provided an adequate description for it. He thereby validated the name, with its priority beginning from 1895. Although Bogin (1955) made a similar analysis, he failed to correct the authorship. The proper authorship should be as follows.

Sagittaria longiloba Engelm. *ex* J.G. Sm., Annual Rep. Missouri Bot. Gard. 6:42. 1895.

ANACARDIACEAE

Rhus hirta

Although Britton (Bull. Torrey Bot. Club 18:269. 1891) indicated that *Datisca hirta* L. (published in 1753) was the earliest name for the staghorn sumac, he believed that transfer of *D. hirta* to the genus *Rhus* would create a later homonym of Harvey's *R. hirta*. We quote from Britton's article: "Although *hirta* is thus the oldest specific name associated with the plant, we are, I think, debarred from using it by the publication of *Rhus hirta* Harv., as a synonym by Engler (in C. DC., *Monogr. Phan.* 4:425. 1883), where this is referred to *R. tridentata*, Sond." Consequently, he accepted the name *R. typhina* L. (published in 1756), for the staghorn sumac. Britton's nomenclatural understanding of the sumac in question was probably appropriate during his time, but inappropriate under the present Code (Greuter *et al.* 1988). Harvey's manuscript's name *R. hirta*, which first appeared in Engler's treatment (as a synonym of *R. tridentata*, an African sumac), was indeed effectively published, but never validly published. Hence, Harvey's manuscript name has no nomenclatural standing (ICBN Art. 34.1). Therefore, contrary to Britton's

belief, the transfer of *D. hirta* to the genus *Rhus* would not have created a later homonym of *R. hirta* Harvey *ex* Engler, *pro syn.*

Sudworth (Bull. Torrey Bot. Club 19:80-81. 1892) argued against Britton's assertion and concluded that *Datisca hirta* could be transferred to the genus *Rhus*. Accordingly, he made the new combination: *Rhus hirta* (L.) Sudworth. In a rejoinder to Sudworth's note [published on the same page that the new combination (*R. hirta*) was published], Britton rejected Sudworth's new combination, but subsequently (in Britton & Brown 1913) accepted the new combination. Sudworth (1927:180) used the name *R. hirta* and remarked about the usage of the binomial *R. typhina* by others. Consistent with Sudworth's remark, many subsequent workers, such as Barkley (1937), Gleason (1952), Radford *et al.* (1968), Little (1979), McGregor (1986), Voss (1985), and Wofford (1989) accepted the name *R. typhina*. In addition to the name *R. hirta* (L.) Sudworth, Barkley (1937:326) also mentioned *R. hirta* "L. *ex* Small" as a synonym of *R. typhina*. On verification, we found that Small (1903) had indeed used the name *R. hirta* and attributed it to Linnaeus. We believe that Small certainly should have been aware of Britton's and Sudworth's notes on the sumac name under consideration and thereafter, should have chosen to follow Sudworth. However, he erred on the authorship in attributing the name to Linnaeus. Likewise, Barkley also erred by attributing the name *R. hirta* to "L. *ex* Small."

In order to legitimately use the name *Rhus typhina*, either it must be conserved over *D. hirta*, or the latter name must be rejected by the Nomenclatural Committee of the ICBN. Dr. Jim Reveal (MARY) has been pursuing the retention of the name *R. typhina*. Until or unless the committee decides in favor of Reveal's proposal (a decision we would not endorse), we accept the name *R. hirta* for the North American flora, and provide the following nomenclatural details.

Rhus hirta (L.) Sudworth, Bull. Torrey Bot. Club 19:81. 1892; Small, *Fl. S.E. U.S.* 1334. 1903. BASIONYM: *Datisca hirta* L., *Sp. Pl.* 1037. 1753.

Rhus typhina L., *Cent. Pl.* 2:14. 1756.

Toxicodendron pubescens

Historically, the following names have been associated with the poison-oak of eastern North America: *Rhus toxicarium* Salisb., *R. toxicodendron* L., *Toxicodendron pubescens* P. Mill., *T. quercifolium* (Michx.) E. Greene, *T. toxicarium* (Salisb.) Gillis, *T. toxicodendron* (L.) Britt., and *T. vulgare* P. Mill. After reviewing the nomenclature for this species, it is apparent that the earliest name for this complex is *R. toxicodendron* L. Unfortunately, this Linnaean epithet can not be transferred to *Toxicodendron*, since it would create a tautonym [*T. toxicodendron* (L.) Britt., an illegitimate name (ICBN Art. 23.4)].

Gillis (1971) presented an informative analysis on the nomenclature of the poison-oak. With reference to the name *Toxicodendron vulgare*, Gillis stated (p. 413): "*Toxicodendron vulgare* is too inaccurately described to be Eastern poison-oak, even though indirectly linked with that species in the literature ..., this binomial must be rejected under (ICBN) Art. 69 of the code." Furthermore, he also rejected the name *T. pubescens* remarking: "His (Miller's) description fits *T. toxicarium* which has pubescent leaves and fruits, but not to the exclusion of all other taxa." (Both rejections are not permissible under the current code.) Consequently, Gillis chose the next earliest name (*Rhus toxicarium* Salisb.), transferred it to *Toxicodendron*, and made the combination: *T. toxicarium* (Salisb.) Gillis. Unfortunately, the basionym *R. toxicarium* is superfluous, since Salisbury cited *R. toxicodendron* in synonymy.

With reference to Gillis' new combination, we analyzed his treatment and concluded the following: Gillis did not exclude the Linnaean type of *Rhus toxicodendron* L. Gillis presumed that *R. toxicarium* had priority and was unaware that it was an illegitimate name and that ICBN Art. 45, Note 2 (pertaining to priority of names) and Art. 49 (pertaining to parenthetical authorship) applied to his new combination (Lanjouw *et al.* 1966). We apply ICBN Art. 72.2, Note 1, and recognize Gillis' "new combination" as a *nomen novum* (i.e., based on the same type as *R. toxicodendron* L. and *R. toxicarium* Salisb., *nomen superfluum*). In other words, *Toxicodendron toxicarium* Gillis is a legitimate name, with priority from 1971.

Barkley (1937) recognized the name *Toxicodendron quercifolium* for the plant in question. (The name *T. quercifolium* was based on *Rhus toxicodendron* var. *quercifolium* Michx.). He rejected the name *T. pubescens* and placed it (in parts) as synonyms of both *T. quercifolium* and *T. radicans* (L.) Kuntze. Barkley's rejection of the name *T. pubescens* was probably appropriate for the Code of his time, but inappropriate under today's Code. For the legitimate use of *T. pubescens*, Reveal (Taxon 40:334. 1991) designated a neotype. In his article, Reveal was correct in his assessment that *T. toxicarium* Gillis is a "new name" but erred in considering it to be "*nom. illeg. superfl.*"

Toxicodendron pubescens P. Mill., *Gard. Dict.*, ed. 8, Art. *Toxicodendron*, no. 2. 1768. NEOTYPE (*vide* Reveal, Taxon 40:334. 1991): Uvedale collection, Sloane herbarium, *H.S.* 315:86 (BM-SL).

Rhus toxicodendron L., *Sp. Pl.* 1:266. 1753. *Rhus toxicarium* Salisb., *Prodr.* 170. 1796. *Toxicodendron toxicodendron* (L.) Britt. in Britt. & Brown, *Ill. Fl. N. U.S.*, ed. 2. 2:484. 1913, *nom. illegit.* *Toxicodendron toxicarium* Gillis, *Rhodora* 73:402. 1971.

Toxicodendron quercifolium (Michx.) E. Greene, *Leaf. Bot. Observ. Crit.* 1:127. 1905.

ASTERACEAE

Madia exigua

In the second note of his article, Gray (Proc. Amer. Acad. Arts 8:372-412. 1872) included a total of 701 numbers, of which the nos. 284-288 pertained to the genus *Madia*. For no. 288 (p. 391), Gray stated: "*Madia* (*Harpecarpus*) *filipes*. *Harpecarpus madrioides* Nutt. This and the related *M. exigua* (*Sclerocarpus exiguus* Smith) form a marked section of the genus expanded."

Cronquist (1955), Kartesz & Kartesz (1980), and Dorn (1988) accepted Gray as the combining author of the name *Madia exigua*, but the Soil Conservation Service (1982) recognized Greene (*Erythea* 1:90. 1893) as the combining author. From Gray's treatment of the name, it is clear that he validly and effectively made the new combination. Any rejection of Gray's usage of the name, as an incidental mention, and thus invalid (Voss *et al.* 1983; ICBN Art. 34.1c), is now incorrect, since the preceding Article was dropped in the Berlin Congress (Greuter *et al.* 1988). Hence, we concur with Cronquist (1955), Kartesz & Kartesz (1980), and Dorn (1988) that Gray is the combining author of the combination.

Madia exigua (Smith) A. Gray, Proc. Amer. Acad. Arts 8:391. 1872. BASIONYM: *Sclerocarpus exiguus* Smith in Rees, *Cycl.* 31. 1815.

FABACEAE

Chamaecrista nictitans

Irwin & Barneby (1982) proposed (among several others) a new combination: *Chamaecrista nictitans* (L.) Moench var. *ramosa* (Vogel) Irwin & Barneby, which was based on *Cassia patellaria* DC. ex Colladon var. *ramosa* Vogel. The authors also cited *Cassia patellaria* as a synonym.

When Vogel proposed his var. *ramosa*, he automatically created the autonym: *Cassia patellaria* DC. ex Colladon var. *patellaria*. It was most likely that Irwin & Barneby followed the Leningrad Congress, which stated that autonyms were not to be taken into consideration for purposes of priority (Stafleu 1978; ICBN Art. 26.2), whereas in the Sydney Congress that principle was reversed, with autonyms having priority over the names that established them (Voss *et al.* 1983; ICBN Art. 57.3). A new combination is therefore needed and is proposed below:

***Chamaecrista nictitans* (L.) Moench var. *patellaria* (DC. ex Colladon) Kartesz & Gandhi, *comb. nov.* BASIONYM: *Cassia patellaria* DC. ex Colladon var. *patellaria*, automatically established by *Cassia patellaria* var. *ramosa* Vogel, 1837. *Cassia patellaria* var. *ramosa* Vogel, *Syn. Gen. Cass.* 66. 1837. *Chamaecrista nictitans* (L.) Moench var. *ramosa* (Vogel) Irwin & Barneby, Mem. New York Bot. Garden 35:817. 1982.**

Lotus unifoliolatus

Lotus purshianus has historically been the scientific name used for the Spanish clover (Hitchcock in Hitchcock & Cronquist 1961; Isely 1981; Barneby 1989); however, Dorn (1988:171) used the name *L. unifoliolatus* Benth. Hitchcock as well as Isely attributed the name *L. purshianus* to "(Benth.) Clements & Clements" and cited the names *L. sericeus* Pursh (a later homonym), *Trigonella americana* Nutt., *Hosackia purshiana* Benth., *H. unifoliolata* Benth., and *L. americanus* (Nutt.) Bisch. (a later homonym) in synonymy. Barneby attributed the name *L. purshianus* to "(Benth. ex Lindl.) F. & E. Clements ex Ottley" but did not include *H. unifoliolata* in synonymy. Under the name *L. unifoliolatus*, Dorn (1988:303) cited *L. purshianus* as a synonym and mentioned the following: "*Lotus purshianus* - *Hosackia purshiana*, on which name was based, is illegitimate. The epithet *americanus* should have been taken up by Bentham." Since Dorn's remarks were brief and since the most recent work of Barneby differed from that of Dorn, we decided to investigate the name *L. purshianus*.

The earliest binomial in this complex appears to be *Lotus sericeus* Pursh, and hitherto, this binomial has been considered to be a later homonym of *L. sericeus* DC. In our study, we found that prior to de Candolle's usage of the name *L. sericeus*, Moench used the binomial *L. sericeus*. Although Moench's binomial was superfluous (he cited *L. creticus* L. as a synonym), and thus illegitimate, it still rendered both de Candolle's and Pursh's binomials to be illegitimate (ICBN Art. 64.1, Note 1).

Regarding the authorship of *Hosackia purshiana*, the name was validly published in Lindley's (Bot. Reg. 15: t. 1257. 1829) work. Possibly for this reason, Barneby (1989) considered Lindley to be the validating author. However, Lindley clearly indicated that Bentham contributed the description of this species; hence, Bentham is the author of the binomial *H. purshiana*. The next question is whether to consider the name *L. purshianus* as a new combination (as did Hitchcock, Isely, and Barneby), as a *nomen novum*, or as a *species novum*.

Clements & Clements (1914:183) used the name *Lotus purshianus* and provided key characters, but did not provide a citation. In their preface, they referenced Britton & Brown (among others), but their key characters were not copied from Britton & Brown (1897, 1913).

Neither Hitchcock (in Hitchcock & Cronquist 1961) nor Barneby (1989) discussed the nomenclature of *Lotus purshianus*, but Isely (1981:243-244) did provide a discussion. Isely contended that Clements & Clements' preface reference to Britton & Brown (who included *Hosackia purshiana* as a synonym of *L. americanus*) should be considered as an indirect reference to Bentham's *H. purshiana*. With this assertion, Isely concluded that Clements & Clements had validly made the combination: *L. purshianus* (Benth.) Clements & Clements.

Our analysis, contrary to Isely's assertion, follows.

Nuttall transferred *Lotus sericeus* to the genus *Trigonella* L. and provided a new name: *T. americana*. Bentham (in Lindley 1829) proposed the name *Hosackia purshiana* for *L. sericeus* and cited *T. americana* as a synonym. Later, Bentham (Trans. Linn. Soc. London. 17:368. 1837) rejected the name *H. purshiana*, accepted the name *L. sericeus*, and cited *T. americana* and *H. purshiana* as synonyms. Since both *H. purshiana* and *T. americana* were based on the type of *L. sericeus*, Bentham should have accepted the epithet *americana* in lieu of the epithet *purshiana*. However, he did not. This rendered the name *H. purshiana* to be superfluous, and thus illegitimate (ICBN Art. 63.1). Moreover, the name *H. purshiana* must not be considered for purpose of priority (ICBN Art. 45.3). Any resultant new combination, based on *H. purshiana*, must be considered as a *nomen novum*, without a parenthetical author (ICBN Art. 72.2, Note 1). Hence, even if Hitchcock, Isely, and Barneby were correct in assuming that the name *L. purshianus* was based on *H. purshiana*, they erred in treating *L. purshianus* as a new combination. Ottley's (1944) usage of the name *L. purshianus* suggested that he considered it to be a *nomen novum* for *L. americanus*. However, we believe that Clements & Clements' usage of the name *L. purshianus* should be considered a *species novum*.

Clements & Clements' preface reference to Britton & Brown (1897) was a generalized statement and was not specific enough to provide even an indirect reference to either Nuttall or Bentham, i.e., the requirements of ICBN Art. 32.4 were never met for an indirect reference to make a *nomen novum* or *combinatio novum*. Regarding the usage of the epithet *purshianus*, perhaps Clements & Clements were aware of Bentham's treatment; however, due to a lack of citation, this speculation can not be verified. The use of the epithet *purshiana* by Bentham as well as by Clements & Clements should be considered coincidental. Therefore, we conclude that Clements & Clements inadvertently, but validly and effectively proposed a new species, with priority from 1914.

With the nomenclature of the name *Lotus purshianus* resolved, additional discussion on Barneby's nomenclature is not made here. We conclude that *L. unifoliolatus* is the correct name for Spanish clover, as indicated by Dorn (1988).

Lotus unifoliolatus (Hook.) Benth., Trans. Linn. Soc. 17:368. 1837. BASYNONYM: *Hosackia unifoliolata* Hook., Fl. Bor. Amer. 1:135. 1833.

Lotus sericeus Pursh, Fl. Amer. Sept. 2:489. 1814, non Moench, 1802, nec DC., 1813. *Trigonella americana* Nutt., Gen. Pl. 2:120. 1818. *Lotus americanus* (Nutt.) Bisch., Linnaea 14(App.):132. 1840, non Vell., 1825. *Hosackia purshiana* Benth. in Lindl., Bot. Reg. 15: t. 1257. 1829, nom. illegit.

Lotus purshianus Clements & Clements, Rocky Mt. Fls. 183. 1914.

The above treatment necessitates the transfer of *L. purshianus* var. *helleri* (Britt.) Isely to *L. unifoliolatus*, for which the following new combination is proposed.

Lotus unifoliolatus (Hook.) Benth. var. *helleri* (Britt.) Kartesz & Gandhi, *comb. nov.* BASIONYM: *Lotus helleri* Britt., Bull. Torrey Bot. Club 17:312. 1890. *Lotus purshianus* Clements & Clements var. *helleri* (Britt.) Isely, Brittonia 30:468. 1928. LECTOTYPE (*vide* Isely, *l.c.*): U.S.A. North Carolina: Mecklenberg Co., 1835, *Curtis s.n.* (NY).

ROSACEAE

Horkelia fusca var. *parviflora*

Dorn (1988) attributed the authorship of *Horkelia fusca* Lindl. var. *parviflora* to (Nutt. *ex* Hook. & Arn.) Peck, whereas the Soil Conservation Service (1982, vol. 2) attributed it to (Nutt. *ex* Torr. & Gray) Wawra. Hence, we decided to research the nomenclature.

Hooker & Arnott (1839) numbered each taxon that they accepted. In the protologue of *Horkelia cuneata* Lindl. (p. 338, no. 2), they mentioned the Nuttalean manuscript name *H. parviflora* and provided a brief description, but did not include this name in the index. Since the name *H. parviflora* was not separately numbered and not indexed, its inclusion in the protologue of *H. cuneata* could be interpreted as either a provisional name (ICBN Art. 34.1b), a described name in synonymy (ICBN Art. 34.1c), or both, none of which can be considered to be legitimate.

Torrey & Gray (1840) independently described *Horkelia parviflora* (attributing the name to Nuttall), and thus validated the name; hence, the correct authorship of *H. parviflora* is: Nutt. *ex* Torr. & Gray. Wawra transferred *H. parviflora* to *H. fusca* at varietal status. Perhaps unaware of Wawra's earlier combination, Peck independently transferred *H. parviflora* to *H. fusca* at varietal status, and attributed the basionym to Hooker & Arnott. Since the type specimen for both Hooker & Arnott and for Torrey & Gray was a Nuttalean specimen, Peck's new combination must be considered as an isonym (Nicolson 1975).

Horkelia fusca Lindl. var. *parviflora* (Nutt. *ex* Torr. & Gray) Wawra, *Itin. Princ. S. Cobungi* 1:17. 1883; Peck, *Madroño* 6:134. 1941. BASIONYM: *Horkelia parviflora* Nutt. [*ex* Hook. & Arn., *Fl. Bor. Amer.* 338. 1839, *nom. invalid*] *ex* Torr. & Gray, *Fl. N. Amer.* 1:435. 1840.

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A NEW VARIETY OF *ERYTHRONIUM CITRINUM* (LILIACEAE) FROM THE
SCOTT MOUNTAINS OF NORTHWEST CALIFORNIA

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ABSTRACT

A new variety of *Erythronium citrinum* S. Watson, the var. **roderickii**, is described from ultrabasic soils in the Scott Mountains, Trinity River drainage, northwest California. It differs from typical *E. citrinum* in having pink to purplish anthers and a brighter yellow zone at the base of the tepals.

KEY WORDS: Liliaceae, taxonomy, *Erythronium*, California

INTRODUCTION

In the course of our study of *Erythronium* for the Jepson Manual Project, a number of interesting collections and field observations dealing with range extensions and potential new taxa have been brought to our attention (Shevock, Bartel, & Allen 1990). The new variety described herein has been known to bulb specialist Wayne Roderick since 1961. In the spring of 1991, Roderick collected herbarium specimens and sent them to the senior author for a more detailed study. We have concluded that this entity is indeed worthy of recognition and we formally describe it here.

TAXONOMY

***Erythronium citrinum* S. Watson var. *roderickii* Shevock & Allen var. nov.** TYPE: UNITED STATES. California: Trinity Co., along California Highway 3, adjacent to Scott Mountain Creek, Trinity River drainage, NE facing slopes on ultrabasic (serpentine) soils, mixed conifer forest, Shasta-Trinity National Forest, T39N, R7W, sect. 15 NW1/4. MDB&M., 4000 ft. (1220 m), 3 May 1991, *Wayne Roderick s.n.* (HOLOTYPE: CAS; Isotypes: JEPS,K,MO,NY,OSC,RSA,UVIC,US).

Tepalis albis, differt a *Erythronium citrinum* S. Wats. var. *citrinum* basibus aureoribus; antheris roseis vel purpureis.

Bulb 3-6 cm long, slender. Leaves 2, strongly mottled, 8-30 mm wide, 5.5-16 cm long, lanceolate to narrowly ovate. Scapes 7.5-16.5 cm tall; flowers 1(-2). Perianth segments recurved, lanceolate, acute to acuminate, 20-35 mm long, 5-8(-10) mm wide, white, fading pinkish after anthesis, with a 5-7 mm long golden yellow zone at base (darker yellow than the typical variety): inner perianth segments with saclike folds at base. Stamens unequal in two series, filaments 8-10 and 10-12 mm long, slender, anthers pink to purple, drying reddish brown, 3-5 mm long. Style clavate, 6-9 mm long, white to cream colored, occasionally tinged pinkish, stigma entire to short lobed, the lobes < 0.5 mm long. Capsules obovoid, 1.5-3.0 cm long.

Specimens examined. UNITED STATES. California: Trinity Co.: from the type locality, (specimen in fruit), 28 May 1991, *Linda Barker 2012* (CAS); Bear Creek Trail, approximately 1 mile W of California Highway 3 near boundary of Trinity Alps Wilderness, T39N, R7W, SE1/4 NW1/4 section 34, (specimen in fruit), 9 June 1991, *Wayne Steffes s.n.* (CAS).

This *Erythronium* first came to our attention in May 1991, although it has been in very limited cultivation since the mid 1970's. We are pleased to name this variety for its discoverer, the noted horticulturist Wayne Roderick, who specializes in California bulbs (Wolf 1986). We propose the vernacular name be Scott Mountains fawn lily.

The Klamath Mountains of northwest California and southwest Oregon contain at least six taxa of *Erythronium*, and are a center of diversity for the genus (Applegate 1935). *Erythronium citrinum* var. *roderickii* is known at present from only three localities, and appears to be a relatively rare localized endemic of this region. There is a high likelihood that continued field work on serpentine soils in the Scott Mountains will yield additional occurrences.

The origins of *Erythronium citrinum* var. *roderickii* are problematic. In most aspects it closely resembles typical *E. citrinum*. However, the anther color suggests the possibility of past hybridization between the cream anthered *E. citrinum* and a purple anthered species, the most likely candidate being *E.*

hendersonii S. Watson. Both typical *E. citrinum* and *E. hendersonii* occur farther north in the Klamath Mountains (Klamath River drainage), and no other *Erythronium* species is currently found in close proximity to *E. citrinum* var. *roderickii*.

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A NEW SPECIES OF *PITCAIRNIA* (BROMELIACEAE: PITCAIRNIOIDEAE)

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ABSTRACT

Pitcairnia ramosii, a new species from Colombia, is described and discussed.

KEY WORDS: Bromeliaceae, Colombia, *Pitcairnia*

Pitcairnia ramosii M.A. Spencer & L.B. Smith, *sp. nov.* Fig. 1. **TYPE:** COLOMBIA. Chocó: Municipio San Jose del Palmar, Cerro del Torrá, vertiente oriental del Río Negro, abajo del helipuerto, vereda del Río Negro, 1630 m, 8 Aug 1988, *J.E. Ramos, P.A. Silverstone, & L.H. Ramos 1052* (HOLOTYPE: CUVCI; Isotypes: MO!, NY!, US!).

A *Pitcairnia lepidopetalone* L.B. Smith affinis, a qua differt, inflorescentia subdense multiflora, pedicelis brevibus, sepalis brevibus margine undulatis et apice rotundatis, petalis apice acutis et luteo-viridis, ovario semisupero.

PLANT caulescent, epiphytic or terrestrial, flowering to 8 dm high. **LEAVES** isomorphic, subdistichous, 10-13 dm long. **SHEATHS** inconspicuous, narrowly oblong, 9-12 cm long and 1.5-2.0 cm wide, entire, densely and minutely brown lepidote. **BLADES** linear-lanceolate, long attenuate, 9-12 dm long and 1.0-2.5 cm wide, plicate, entire, glabrous above, sparsely and minutely brown lepidote below, slightly narrowed at the base but not petiolate. **SCAPE** erect, slender, 6.5-7.0 dm long and 5-7 mm in diameter, glabrous. **SCAPE BRACTS** strict, the lower subfoliaceous and exceeding the internodes, the upper broadly ovate with an acuminate apex, 20-25 mm long and 15-20 mm wide, slightly shorter than to equaling the internodes, entire, membranaceous, light yellow-green. **INFLORESCENCE** simple, subdensely 15-25 flowered, racemose, 10-15 cm long and 5-7 cm in diameter, glabrous. **FLORAL BRACTS** spreading, ovate



Figure 1. Holotype of *Pitcairnia ramosii*, Chocó, Colombia.

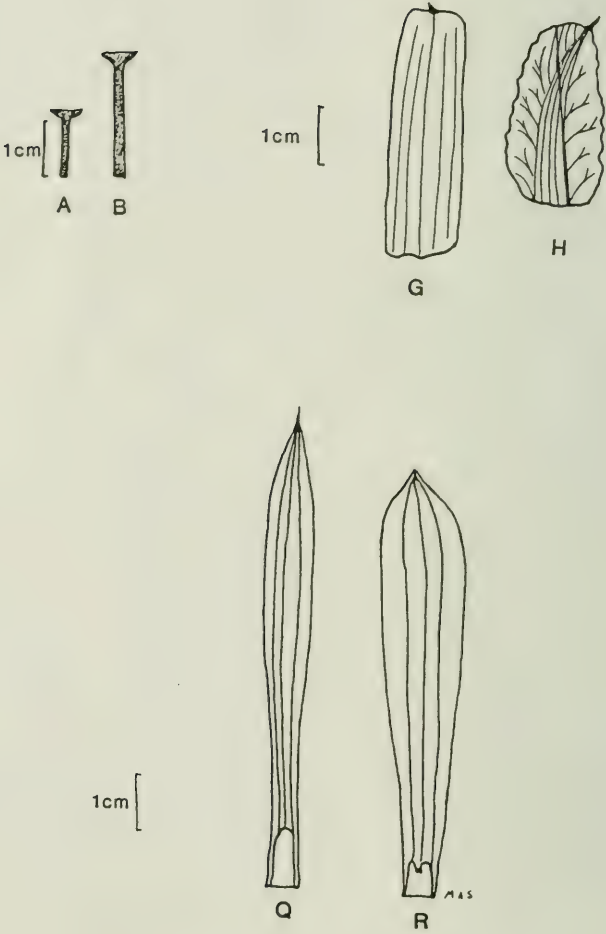


Figure 2. *Pitcairnia ramosii*: A, pedicel; H, sepal; R, petal. *Pitcairnia lepidopetalon*: B, pedicel; G, sepal; Q, petal.

with an acuminate apex, 20-25 mm long and 15-20 mm wide, inflated, undulate, entire, membranaceous, much exceeding the pedicels, light yellow-green. FLOWERS spreading. PEDICELS slender, 10 mm long and 1 mm in diameter, glabrous. SEPALS slightly asymmetric, oblong, rounded and apiculate, 32 mm long and 15 mm wide, alate-carinate, membranaceous, entire, undulate, sparsely and minutely stellate lepidote, light green with a bright red apex before anthesis, turning light green with only a small, dark purple spot at the apex by anthesis. COROLLA zygomorphic. PETALS lingulate, acute, 70 mm long and 10 mm wide, sparsely white lepidote, bearing a single, erose-undulate ligule at the base, white becoming light green at apex. STAMENS included, 65 mm long. FILAMENTS free, linear, 54 mm long and 0.5 mm wide. ANTHERS linear, 11 mm long and 1 mm wide, basally dorsifixed, yellow. PISTIL included. STYLE terete, 55 mm long and 1 mm in diameter. STIGMA 5 mm long, lobes unequal, loosely spiraled. OVARY spheroidal, 5 mm long and 5 mm in diameter, 1/2 superior. OVULES long caudate.

OTHER SPECIMENS EXAMINED: COLOMBIA. Chocó: Municipio San Jose del Palmar, Cerro del Torrá, vertiente nordeste, bosque de neblina, 1850-1930 m, 13 Aug 1982, *Felipe Silverstone-Sopkin 1941* (CUVC, MO!).

DISCUSSION: The presence of caudate ovules places this new species in *Pitcairnia* subgenus *Pitcairnia* (Smith 1974).

Pitcairnia ramosii is most closely related to *P. lepidopetalon* L.B. Smith but can be distinguished from the latter by its subdensely many flowered inflorescence, shorter pedicels, slightly asymmetric and shorter sepals that have undulate margins and a rounded apex, yellow-green petals that have an acute apex, and semisuperior ovary. In *P. lepidopetalon*, the inflorescence is lax and few flowered, the pedicels are twice as long, the sepals are longer, symmetric, the margins are even and the apex is truncate, the petals are red with an attenuate apex, and the ovary is 2/3 superior.

Both *Pitcairnia ramosii* and *P. lepidopetalon* are known only from the moist, montane forests of eastern Colombia.

ETYMOLOGY: This new species is named in honor of the collector, Dr. Jorge E. Ramos, Universidad De Valle, Cali, Colombia.

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UNION OF *BRADBURIA* WITH *CHRYSOPSIS* (ASTERACEAE: ASTEREAE),
WITH A PHYLOGENETIC HYPOTHESIS FOR *CHRYSOPSIS*

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ABSTRACT

The monotypic genus *Bradburia* (*B. hirtella* Torrey & Gray) is merged with *Chrysopsis* (as *C. texana* *nom. nov.*), enlarging the latter to eleven species. Within *Chrysopsis*, *C. texana* and *C. pilosa* are sister species, based on a set of distinctive features common to both taxa. Both species are the westernmost of the genus and (as *Chrysopsis* sect. *Bradburia* *comb. et stat. nov.*) they form a group phyletically coordinate with the other species, which are centered in the southeastern United States. A phylogenetic hypothesis is presented for all species of *Chrysopsis*; the genera most closely related to it are *Osbertia* and *Noticastrum*.

KEY WORDS: *Bradburia*, *Chrysopsis*, *Osbertia*, *Noticastrum*, Asteraceae, Astereae

The taxonomic history of the monotypic genus *Bradburia* Torrey & Gray has been summarized by Semple & Chinnappa (1984). Essentially, it has been recognized as closely related to the genera *Heterotheca* Cass. and *Chrysopsis* (Nutt.) Ell., but it differs prominently from both in its sterile disc flowers. The dimorphic achenes of *Heterotheca* (*sensu* Semple 1977; Semple *et al.* 1980) have been noted by some authors as similar, and perhaps homologous, to those of *Bradburia*, but Semple (1981) has observed that a closer relationship exists between *Bradburia* and *Chrysopsis*, in his more restricted view of the latter. Semple (1981, p. 339), indeed, placed the relationship so close that he hypothesized that some isolated, immediate precursors of *C. pilosa* Nutt. "ultimately evolved into *Bradburia hirtella*."

Semple & Chinnappa (1984, p. 95) noted that "While *Bradburia hirtella* could be transferred to *Chrysopsis*, the distinctive staminate florets of the former are considered sufficient to separate the two at the generic level." Later in

the same paper (p. 100), they commented that "The distinctive achene morphology, somewhat different flavonoid pattern, and karyotype support maintenance of *Bradburia* as a genus separate from *Chrysopsis*." The data from the flavonoid studies, however, were not presented in their study, and its authors noted in the same paper (p. 95) that "Flavonoid patterns in the two genera were similar but did not confirm or refute a close relationship."

CHROMOSOMES

Detailed studies of meiotic pairing in *Chrysopsis* hybrids (Semple & Chinnappa 1980a) and of chromosome numbers and karyotypes (Semple & Chinnappa 1980b) showed that four basic karyotypes exist within *Chrysopsis*: the $x = 4$ of *C. pilosa*, the $x = 4$ of *C. mariana* (L.) Ell., the $x = 5$ of the majority of the species, and the $x = 9$ of *C. gossypina* (Michx.) Ell. The latter comprises "little more than a combination of the $x = 5$ karyotype and the $x = 4$ *mariana* karyotype and was therefore of allopolyploid origin." (1980b, p. 164). These two studies provided convincing evidence of strong homology between the $x = 4$ *mariana* and the $x = 5$ karyotypes, the former probably derived by loss of chromosome "V" of the $x = 5$ set, with transfer of portions of that chromosome to both chromosomes "II" and "III" of the $x = 4$ *mariana* set. Semple & Chinnappa (1980b, p. 170) hypothesized that the "evolution of the $x = 4$ [*pilosa*] karyotype from the $x = 4$ [*mariana*] karyotype resulted in a considerable increase in asymmetry and an increase in the number of acrocentric homologues" but noted (p. 168) that "no clear homologies [between these two $x = 4$ karyotypes] are suggested by chromosome size and centromere position."

Plants of *Bradburia* have a chromosome number of $n = 3$ over most of the geographic range of the species, but Semple & Chinnappa (1984) reported the significant discovery of an individual with $n = 4$ from the southwesternmost portion of the range. They presented a detailed study of the karyotypes of the two *Bradburia* cytotypes and an artificially synthesized hybrid between the two. In comparing the $n = 4$ chromosome complement of *Bradburia* with that of *Chrysopsis pilosa*, they observed (p. 100) that "if the large pair of the *C. pilosa* karyotype was more metacentric, then the karyotype would be superficially very similar to that of the $n = 4$ karyotype of *Bradburia*." Based on their very clear photographs and diagrams, the phrase "superficially very similar" could be replaced by "virtually identical." Semple & Chinnappa (p. 99) further noted that comparison of their karyotypes "suggests a possible origin of *Bradburia* from an early ancestor of *C. pilosa*." They did not offer a precise hypothesis of how the $n = 3$ complement originated from the $n = 4$, but clearly the two may be interpreted as homologous.

MORPHOLOGY

Phylogenetic analyses of the goldenaster lineage (Nesom 1991a) and of the genus *Chrysopsis* (see details below) indicate that *Bradburia* is closely related to *Chrysopsis*, based on their thin walled and vitreous upper cells of the Type A trichomes, and distinctive achene morphology (obovate, with thick, buried ribs). Among the species of *Chrysopsis*, it is similar to *C. pilosa* in its chromosome number, karyotype (see discussion above), annual duration, spring flowering, long flowering branches, Type A trichomes with the distal cells thin walled but not elongated into a flagelliform terminal portion, phyllaries with broad scarious margins, lack of characteristically large, elongated crystals in the tissues of the disc corolla throat, sharp pointed sweeping hairs on the disc style branches, and ray corollas remaining straight rather than coiling. Together these similarities provide evidence that the two taxa are related as sister species.

Despite its close relationship to *Chrysopsis pilosa*, *Bradburia* differs from it in a number of features. The difference that has been heavily emphasized is the sterility of disc ovaries and concomitant reduction of the disc pappus to two awns. Additionally, the ray achenes of *Bradburia* are 3 sided, the outer face distinctly broadened (vs. merely 2 sided in *C. pilosa*), with an outer pappus composed of a whorl of relatively inconspicuous, short bristles and setae (vs. a whorl of broad scales); the pappus bristles of *Bradburia* are distinctly flattened and characteristically reddish near the base (vs. terete and tawny); the leaves of *Bradburia* are narrow at the base and strictly sessile (vs. basally broadened and subclasping); the heads of the glandular (Type C) trichomes are broader (5-8 cells across vs. 3-5 cells); and the phyllaries are essentially glabrous (vs. distinctly hairy glandular). Attempts to cross *Bradburia* with *C. pilosa* have been unsuccessful (Semple & Chinnappa 1984), and populations of the two species are sometimes intimately intermixed in nature (Nesom personal observ.).

While the differences that separate *Bradburia* from *Chrysopsis pilosa* are at least as great as those that distinguish most other species of *Chrysopsis*, Semple (1981, p. 338) noted that *C. pilosa* itself is "the most divergent species [of the genus] in terms of morphology, chemistry, and cytology." Further, *C. pilosa* and *Bradburia* are so distinct as a pair that *C. pilosa* might justifiably be transferred to *Bradburia*, but the similarity in achene morphology between them and the other species of *Chrysopsis* strongly suggests that the group as a whole is monophyletic and should stand as a single genus. Artificially produced hybrids between *C. pilosa* and *C. gossypina* (Semple 1981) emphasize a significant degree of genetic similarity between the two segments of the genus. No one has suggested that *C. pilosa* be formally recognized apart from the other species of the genus; if it is taxonomically treated as *Chrysopsis*, then so should *Bradburia*. The close relationship between these two species, apart

from the rest of the genus, is formalized in the nomenclature below.

Chrysopsis sect. **Bradburia** (Torrey & Gray) Nesom, *comb. et stat. nov.*

BASIONYM: *Bradburia* Torrey & Gray, *Fl. N. Amer.* 2:250. 1842.

Species included: *C. pilosa* Nutt. and the type species:

Chrysopsis *texana* Nesom, *nom. nov.* BASIONYM: *Bradburia hirtella*

Torrey & Gray, *Fl. N. Amer.* 2:250. 1842; not *Chrysopsis hirtella* DC., 1836. TYPE: UNITED STATES. Texas: [no other data], *Drummond 134* (HOLOTYPE: not seen; Probable isotype: LL!).

CLADISTIC ANALYSIS

In a broader cladistic study that includes all of the goldenasters (Nesom 1991a), *Osbertia* ($x = 5$) E. Greene of México and Central America and *Noticastrum* DC. ($x = 9$) of South America are hypothesized to be the closest relatives of *Chrysopsis* (including *Bradburia*), based on their relatively long, smooth, thin walled, and vitreous Type A trichomes. In order to determine the phylogenetic position of *Bradburia*, it has been included in a phylogenetic analysis of the species of *Chrysopsis*, with the assumption that such a group is holophyletic only with the inclusion of *Bradburia*. The closely related goldenaster genus *Heterotheca* has been added as part of the outgroup to clarify some of the character state polarities.

Studies of microcharacters were made with a compound microscope using epidermal "skims" with a razor from stems and slides of dissected flowers mounted in Hoyer's Medium. A list of specimens from which slides have been made is deposited at TEX; all voucher specimens are deposited in TEX. All specimens examined and scored of *Bradburia* presumably have a chromosome number of $n = 3$. Characters and character states used in the analysis are given in Table 1; coding for the individual taxa are in Table 2; discussion of variability in the characters used is provided in the Appendix. The data were analyzed using PAUP (Swofford 1985) with Wagner parsimony. *Chrysopsis gossypina* was not included in the analysis, since it apparently is of hybrid origin (Semple 1980b); its position relative to the other species is shown on the cladogram following Semple (1981).

A single shortest tree of 42 steps (Fig. 1) accounts for the distribution of character states among the taxa included in the analysis. *Chrysopsis texana* (*Bradburia*) and *C. pilosa* (sect. *Bradburia*) are geographically the westernmost of the genus and form a clade phyletically coordinate with the other species (sect. *Chrysopsis*), which are centered in the southeastern United States. In contrast to Semple (1981), who placed the ancestor of the whole genus in

TABLE 1. Characters and character states

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1. Chromosome number, (0) $n = 4$ or 3, the "pilosa" karyotype, or $n = 9$ (1) $n = 5$ or 4, the "*Chrysopsis*" karyotype
 2. Chromosome number, (0) $x = 5$ or 4, the "mariana" karyotype or its $n = 5$ homologue, or $n = 9$ (1) $n = 4$ or $n = 3$, the "pilosa" karyotype
 3. Chromosome number, (0) $n = 4$ or $n = 3$, the "pilosa" karyotype, or $n = 9$ or $n = 5$ (1) $x = 4$, the "mariana" karyotype
 4. Duration, (0) perennial or biennial (1) annual
 5. Flowering phenology, (0) primarily in late summer and fall, rarely in the spring (1) typically beginning in the spring, often continuing into the fall
 6. Rhizomes/roots, (0) rhizomes (1) taproots
 7. Capitulescence, (0) loosely to compactly corymbose (1) monocephalous
 8. Flowering branch length, (0) relatively short, arising from the upper third of the stem, or the stems monocephalous (1) relatively long, commonly arising from the lower half of the stem
 9. Leaf insertion, (0) clasping or subclasping (1) not at all clasping
 10. Vestiture of peduncles and phyllaries, (0) stipitate glandular (1) glandularity absent or highly reduced
 11. Type A trichomes, (0) terete with thick, papillate walls (1) terete to flattened with thin, smooth walls
 12. Type A trichome length, (0) relatively short, not at all flagelliform (1) all flagelliform, with the distal cells greatly elongated, at least in some species
 13. Phyllary midvein, (0) mostly included within lamina (1) prominently raised-swollen, orange glandular
 14. Phyllary margins, (0) scarious rim narrow or absent (1) scarious rim very broad
 15. Phyllary apex, (0) attenuate or linear-attenuate (1) blunt-acute
 16. Phyllary apex, (0) attenuate or blunt-acute (1) linear-attenuate
 17. Behavior of buds, (0) erect (1) nodding

TABLE 1. (continued).

18. Ray color, (0) yellow, drying yellow (1) yellow or creamy white, drying yellow tinged with red
 19. Ray corolla behavior after stigma receptivity, (0) coiling (1) remaining straight
 20. Sweeping hair shape, (0) narrowly oblong or slightly broadened apically (1) distinctly lanceolate, at least those near the apex
 21. Sweeping hair apex, (0) narrowly oblong to lanceolate, without a sharp point, or narrowly acute with a sharp point (1) broadly acute with a sharp point
 22. Sweeping hair apex, (0) narrowly oblong to lanceolate, without a sharp point, or broadly acute with a sharp point (1) narrowly acute with a sharp point
 23. Elongate crystals in the tissues of the disc corolla throat, (0) present (1) absent or greatly reduced in size
 24. Resin ducts in disc corolla lobes, (0) continuous or absent (1) discontinuous
 25. Radial walls of cells of upper throat of disc corollas, (0) straight (1) broadly sinuate
 26. Achene walls, (0) eglandular, or with thin, barely raised glandular ridges (1) with thick, raised, glandular ridges
 27. Achene shape, (0) narrowly elliptic to oblanceolate in side view (1) obovate
 28. Achene compression, (0) distinctly compressed (1) terete or subterete
 29. Achene nervation, (0) thin, superficial (1) thick, beneath the surface
 30. Pappus insertion, (0) at shoulder rim of achene apex (1) inset from shoulder rim of achene apex
 31. Pappus series, (0) double (1) single
 32. Outer pappus, (0) setae or absent (1) scales
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TABLE 2. Data matrix for *Osbertia*, *Bradburia*, and the diploid species of *Chrysopsis*.

Taxa	Character State							
<i>Heterotheca</i> (HETERO)	00000	100?0	00000	0?000	00000	00000	00	
<i>Noticastrum</i> (NOTICA)	0000?	?1001	11000	0?110	00000	00000	00	
<i>Osbertia</i> (OSBERT)	?0000	01000	10000	00110	00001	00100	10	
<i>Bradburia</i> (BRADBU)	01011	10110	10010	00011	10101	01011	00	
<i>Chrysopsis pilosa</i> (PILOSA)	01011	10100	10010	00011	10101	01011	01	
<i>C. mariana</i> (MARIAN)	10100	00000	11000	00001	00000	01011	01	
<i>C. lanuginosa</i> (LANUGI)	10000	10000	11000	11001	00000	01011	00	
<i>C. godfreyi</i> (GODFRE)	10000	10000	11000	11001	00000	01011	00	
<i>C. floridana</i> (FLORID)	10000	10000	11001	00001	01000	01011	00	
<i>C. scabrella</i> (SCABRE)	10000	10000	11001	00001	01000	01011	00	
<i>C. latisquamea</i> (LATISQ)	10000	10010	11100	00000	00010	11011	00	
<i>C. linearifolia</i> (LINEAR)	10000	10011	11100	00001	00010	11011	00	
<i>C. subulata</i> (SUBULA)	10001	10011	11100	10001	00010	11011	00	

Florida, the present analysis suggests that such an ancestor, derived from Latin American precursors, probably migrated northward into south central and southeastern North America. The initial divergence, which occurred in the south central region, separated the two major lineages. The species of sect. *Chrysopsis* form four main clades. The relationship among them has not been resolved despite a detailed search for potentially useful characters, but on the basis of their karyotype and long flagelliform hairs, these species are united as a group distinct from sect. *Bradburia*. The morphological data suggest that the ancestor to sect. *Chrysopsis* may have been more or less simultaneously fragmented into four lineages.

The base chromosome number of ancestral *Chrysopsis* is most parsimoniously $x = 9$ in the present hypothesis, but the lack of any primitively $n = 9$ species of *Chrysopsis* and the geographic proximity of the closely related *Osbertia* (Nesom 1991b), with its base chromosome number of $x = 5$, suggests that it, rather than *Noticastrum*, may be phyletically coordinate with *Chrysopsis* and that the primitive number for *Chrysopsis* is $x = 5$. If *Osbertia* and *Chrysopsis* are positioned as sister genera, with *Noticastrum* primitive to both, only two steps are added to the cladogram in Fig. 1, both as easily conceivable parallelisms in characters 7 and 18. A study of the karyotype of *Osbertia* will be critical in further assessing its relationship to *Chrysopsis*.

Whatever may prove to be true regarding the base chromosome number for the immediate ancestor of *Chrysopsis*, within the genus the evolutionary attainment of four pairs of chromosomes in *C. mariana* appears to have oc-

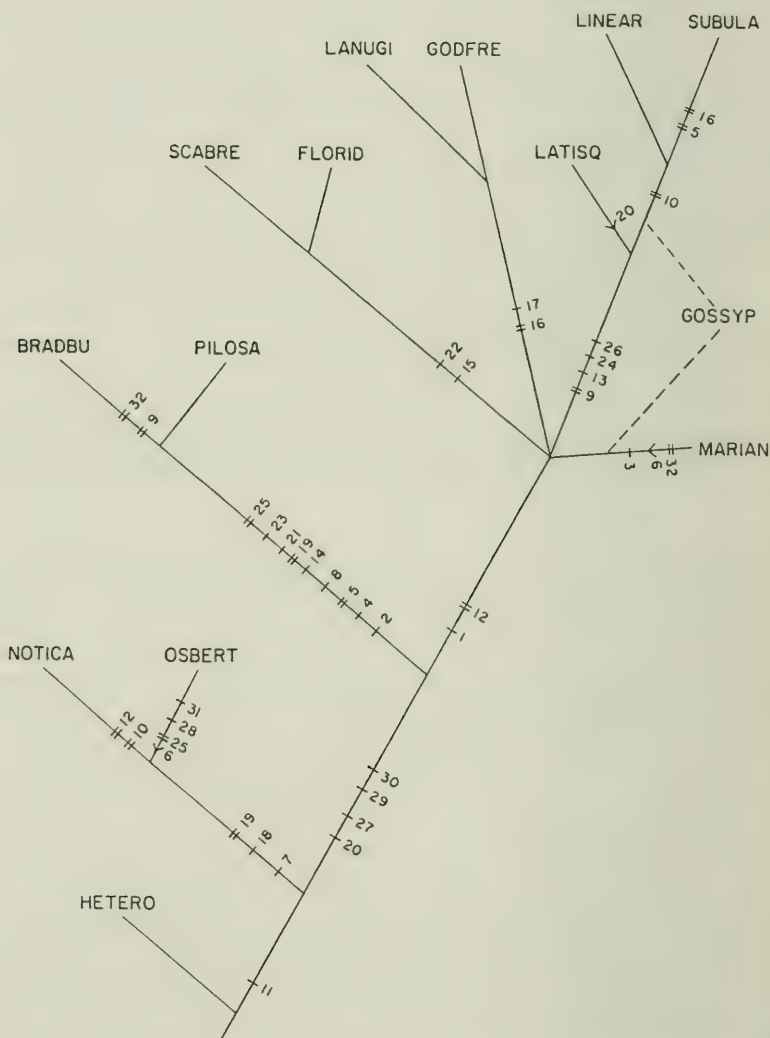


Figure 1. Phylogenetic reconstruction of the *Chrysopsis* lineage and the species of *Chrysopsis*, including *Bradburia*. Abbreviations for the tax follow those in Table 2; "GOSSYP" is *C. gossypina* (see text); "BRADBU" is *C. tezana*. Single slash = apomorphy or autapomorphy; double slash = parallelism; downward arrow = reversal.

curred independently of that in the ancestor of *C. pilosa* and *C. texana*. Even if characters related to chromosomes (characters 1, 2, and 3) are deleted from the analysis, the topology of the resulting cladogram is no different from that in Fig. 1. This supports the hypothesis that the $x = 4$ *pilosa* and the $x = 4$ *mariana* karyotypes are not homologous.

The phylogenetic hypothesis presented here for *Chrysopsis* is similar to the one developed more intuitively by Semple (1981, Figure 3, p. 331). Apart from the general methodology of its construction, without the use of an outgroup for the polarization of character states and without the inclusion of *Bradburia*, Semple's diagrammed hypothesis differs primarily in its indication that *C. pilosa* and *C. mariana* are sister species (based on their reduced chromosome number) and the placement of *C. scabrella-floridana* and *C. lanuginosa-godfreyi* in a single clade (apparently based on geography and what are interpreted here as shared plesiomorphies). The narrative evolutionary scenario for the genus related by Semple (1981) differs from his diagram. In the narrative, he postulated that the divergence of the *latisquamea* lineage and the *scabrella-lanuginosa* lineage from the ancestor of the genus was the first cladistic event, followed by the divergence of the $x = 4$ lineage (including *C. pilosa* and *C. mariana*) from the *scabrella-lanuginosa* lineage. In the narrative, also, he hypothesized that some populations of the immediate precursor of *C. pilosa*, as it migrated from the Florida region toward the Ozark Plateau, became isolated and evolved into *Bradburia*.

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APPENDIX 1. Notes on character variation.

- 1, 2, and 3. Chromosomes: see discussion in text. The scoring relies on data furnished by Semple & Chinnappa (1980b, 1984).
4. Duration: Semple & Chinnappa (1984) observed that the $n = 4$ plants of *Bradburia* lived for 2 1/2 years, as opposed to the strictly annual $n = 3$ ones. This species is scored here as annual, but it would not change the results if it were scored as perennial.
5. Flowering phenology: data from Semple (1981).
6. Rhizomes/roots: some species of *Noticastrum* are rhizomatous, others taprooted; the genus is scored ambiguously, but even if it were not, the topology of the cladogram would not change. The primitive condition of the goldenaster root system is not clear (Nesom 1991a), but *Heterotheca*, which is used as the outgroup in the present analysis, is apparently primitively taprooted.
7. Capitulescence: in *Osbertia* and nearly all species of *Noticastrum* the stems are monocephalous, but some plants of *N. marginatum* (Kunth) Cuatr. produce loose cymes, with several head-bearing branches arising on the upper third of the initial stem. The same is true for *O. bartlettii* (S.F. Blake) Nesom.

Such variants probably reflect the ancestral condition for these two genera, displayed with a release of the suppression of lateral branches.

8. Head bearing branches: in most of *Chrysopsis*, as well as in the genus *Heterotheca*, the capitula are produced on relatively short peduncles originating from a branch point on the upper part of the main stem. In *C. pilosa* and *C. texana*, the peduncles are usually longer and originate from lower portions of the stem.

9. Leaf insertion: in *Bradburia* as well as the three species of the *C. latisquamea* Pollard lineage, the leaves are clearly sessile; in *C. scabrella* Torr. & Gray, *C. floridana* Small, *C. lanuginosa* Small, and *C. godfreyi* Semple, they are clearly clasping or subclasping. Semple (1981) described leaf insertion in *C. pilosa*, *C. mariana*, and *C. scabrella* as sessile, but these species are more similar in leaf base to the clasping leaved species than to the sessile leaved ones.

11 and 12. The smooth, thin walled Type A trichomes that are often lengthened into a tomentose vestiture are the primary feature that distinguishes the *Chrysopsis* lineage from all of the other goldenasters (Semple *et al.* 1980; Nesom 1991a). Type A trichomes in *Noticastrum* are variable in length from species to species, but in some they are minutely flagelliform and form a dense tomentum identical to that of *Chrysopsis* species. The comparatively high degree of variability in vestiture, as well as habit, among the species of *Noticastrum* is perhaps reflective of the ancestral stock of the whole *Chrysopsis* clade. In the cladistic hypothesis offered here, the relatively short hairs of *C. pilosa* and *C. texana* are more primitive than the long flagelliform, tomentum forming hairs characteristic of the other species of *Chrysopsis*.

13. Phyllary midvein: the phyllaries of *C. subulata* Small and *C. linearifolia* Semple are distinctive in their prominently raised-swollen, orange glandular midveins. The midveins of the other species are somewhat variable but none approach the distinctive morphology of these two species.

15 and 16. Phyllary apex: these features are difficult to characterize with precision, but there appear to be two pairs of species, each pair with phyllary apices distinctive from all other species.

17. Behavior of buds: data for *Chrysopsis* from Semple (1981). Comparative data for most of the rest of the goldenaster lineage is lacking, but the buds of the species of *Heterotheca* sect. *Heterotheca* are nodding.

18. Ray color: among the 12-13 species of *Noticastrum*, only *N. acuminatum* (DC.) Cuatr. has rays that are distinctly yellow when fresh. The other species are noted by collectors as having white to dark lavender rays. Upon drying, however, the rays of seven of the eight species I have studied are a densely opaque, dark orangish yellow, sometimes retaining a purplish tinge. The "dry" color of the rays, with a reddish purple tinge, is similar among the other goldenasters only to that in *Osbertia*. Based on these observations and the distribution of other character states in the present analysis, the white

ray color in *Noticastrum* is interpreted here as derived from the primitive yellow rays of the ancestral goldenaster; the yellow rays of *N. acuminatum* have retained the primitive color.

19. Ray corolla behavior after stigma receptivity: the corollas of post-receptive ray flowers in nearly all genera of the goldenaster lineage tightly coil inward, with the adaxial surface exposed. Only in *Noticastrum*, *Osbertia*, *Chrysopsis pilosa*, and *C. texana*, do they remain straight. In the hypothesis here, the noncoiling behavior of first two apparently has evolved in parallel with that of the second two, perhaps reflecting an inherited tendency. In other species of *Chrysopsis* the tendency to coil may be more weakly expressed than in other goldenasters, but it is clear nevertheless. This behavior can be easily observed even on herbarium specimens; I have also observed *C. pilosa* and *C. texana* in the field and in cultivation. Comparative observations for other species are not available, but in *C. pilosa* and *C. texana*, the ray corollas close upwards in parallel at night, forming a narrow pyramid, spreading the next morning.

20, 21, and 22. Sweeping hair shape and apex: in contrast to the rest of the goldenasters, there is a definite tendency in *Chrysopsis* for the sweeping hairs of the disc style appendages to be lanceolate rather than narrowly oblong, at least near the appendage apex. In two pairs of species this tendency is markedly more pronounced than the other species: in *C. texana* and *C. pilosa*, the sweeping hairs are broadly lanceolate to nearly triangular with sharp points; in *C. scabrella* and *C. floridana*, they are linear-lanceolate with sharp points. These two specialized morphologies do not appear to be strictly homologous. Outside of the goldenasters, lanceolate hairs occur in some species of the *Aster* L. lineage, and the sweeping hair apices of some genera of the *Machaeranthera* Nees lineage show the same tendency to be sharp pointed (Nesom in prep.).

23. Elongate crystals in the tissues of the disc corolla throat: relatively large, elongate, straight sided crystals are found in the throat cells of all species of goldenaster except *Chrysopsis texana* and *C. pilosa* (see Nesom 1991a for further details). The corolla throats of *C. pilosa* produce a mixture of stellate "sand" crystals and elongate crystals but the latter are markedly smaller, apparently through reduction, than those in other goldenaster species. *Chrysopsis texana* produces only "sand" crystals.

24. Resin ducts in disc corolla lobes: in the three species of the *latisquamea* lineage, the yellow-orange resin ducts associated with the veins are sharply discontinuous. This is much less pronounced in *C. latisquamea* than in the other two species.

25. Radial cell walls: the difference between the sinuate walls and straight walls can be easily seen in the cells of the upper throat of the disc corollas. Outside of the goldenasters, sinuate walls are particularly characteristic of the disc corolla throats in some groups of *Aster* (Nesom in prep.) as well as related genera.

26, 27, 28, 28, and 30. Achene morphology: the flattened, obovate achenes of *Chrysopsis* (including *C. pilosa* and *Bradburia*) with subepidermal ribbing, truncate apices and inset pappus insertion are distinctive. Raised, orange, glandular ridges occur in the three species of the *latisquamea* lineage and in *C. gossypina*; similar but much thinner and barely raised ridges occur in *Heterotheca* sect. *Heterotheca*, where they appear to have arisen independently as a specialization within that genus. Relatively long achenes with numerous, superficial nerves appear to be primitive within the goldenasters, but the degree of compression is more evolutionarily plastic and less useful in reconstructing phylogeny. The achenes of *Heterotheca* sect. *Ammodia*, for example, are distinctly flattened; those of some species of *Noticastrum* also are strongly compressed, while others are intermediate in compression between *Chrysopsis* and *Osbertia*. In the present analysis, only *Osbertia* is scored as having terete achenes within the *Chrysopsis* lineage.

The achenes of *Bradburia* are strongly 3 sided, at first sight very different from other taxa of *Chrysopsis*, but ray achenes that are slightly but distinctly 3 sided, in exactly the same way as *Bradburia*, are produced by *C. mariana*, *C. scabrella*, and *C. lanuginosa*, although apparently not by *C. pilosa*.

31 and 32. Pappus: *C. pilosa* has an outer series of broad and conspicuous scales. The outer series in *C. mariana* is also more scalelike than the other species of *Chrysopsis* but less pronounced than in *C. pilosa*. The analysis here indicates that the broad wings of the nearly scalelike pair of bristles of the sterile disc achenes in *C. texana* may be homologous with the scales of *C. pilosa*. The scaly outer pappus in some taxa of *Heterotheca* sect. *Heterotheca* is interpreted to have arisen as a specialization within that genus and in parallel with that in *Chrysopsis*. Among the goldenasters, a uniseriate pappus occurs only in *Osbertia*, where it is clearly derived.

TRANSFER OF *ASTER KINGII* TO *TONESTUS* (ASTERACEAE:
ASTEREAE)

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ABSTRACT

Aster kingii is not accommodated in *Machaeranthera* or *Xylorhiza*, the only genera outside of *Aster* with which it has been formally aligned. Studies have returned it to *Aster*, its original position, but it has not been accepted even there in recent taxonomic overviews. Placements alternative to *Aster* have not been suggested by previous workers. Although it is white rayed, the species is transferred here to the primarily yellow rayed genus *Tonestus*, where it is hypothesized to be most closely related to the rayless *T. aberrans*. The new combinations required are *T. kingii* (D.C. Eaton) Nesom and *T. kingii* var. *barnebyana* (Welsh & Goodrich) Nesom.

KEY WORDS: *Tonestus*, *Aster*, *Machaeranthera*, Asteraceae, Aster-eae

Aster kingii D.C. Eaton, a species restricted to the Wasatch and Canyon Mountains of central to north central Utah, has been unsettled in its systematic placement in the last 35 years. It was accepted by earlier North American taxonomists within the bounds of the large and variable genus *Aster* L., but Cronquist & Keck (1957) excluded the species from *Aster* and placed it in their expanded version of *Machaeranthera* Nees (within sect. *Xylorhiza* [Nutt.] Cronq. & Keck series *Integrifoliae* Cronq. & Keck). These authors noted (p. 233) that "The monocephalous montane true perennial '*Aster*' *kingii* D.C. Eaton is suggestive of *Xylorhiza glabriuscula*, but the involucre is that of *Machaeranthera*, and the plant blooms in late summer like other *Machaerantherae*."

The species of *Machaeranthera* sect. *Xylorhiza* are now treated as the genus *Xylorhiza* Nutt., mostly following the monograph by Watson (1977). *Aster kingii*, however, was noted by Watson (1978, p. 209) to be "phenologically, ecologically, morphologically, and chromosomally anomalous ..." within *Xylorhiza*, while he observed resemblances in various features between *A. kingii*

and *A. alpigenus* (Torr. & Gray) A. Gray (in habit), *A. conspicuus* Lindl. (in phyllary morphology), and *A. integrifolius* Nutt. (in vestiture), although in 1977 he had suggested that it might prove to belong to *Machaeranthera* sect. *Machaeranthera*. Welsh (1983) accepted Watson's later point of view and treated the species as *Aster*, transferring a varietal taxon (var. *barnebyana*, see below) named in *Machaeranthera* to a position in *Aster*. In a taxonomic conspectus of the genus *Machaeranthera*, Hartman (1990) also excluded *A. kingii*, leaving it in *Aster*, although he did not provide a commentary regarding its possible affinities there. In contrast, recent taxonomic and phyletic overviews of the genus *Aster* (Jones 1980; Semple & Brouillet 1980; Jones & Young 1983) did not provide a position for *A. kingii* or even a mention of it in any context, although Dr. Jones (pers. comm.) now accepts it as a species of *Aster* sect. *Oreostemma* (E. Greene) Peck.

The chromosome number of *Aster kingii* ($n = 9$ pairs; Watson 1978, for var. *kingii*; Sanderson *et al.* 1984, for var. *barnebyana*) contrasts with all species of *Xylorhiza* ($x = 6$) as well as those of *Machaeranthera* ($x = 4, 5$). Species in groups of *Aster* hypothesized by Jones & Young (1983) to be primitive within the genus have a base chromosome number of $x = 9$, and this is presumably the area where *A. kingii* would find its closest phyletic affinities were it established that it lies within that lineage.

Aster kingii might be left in a broadly conceived *Aster* but its placement there would remain anomalous, as even in that heterogeneous group there are no species to which it can be unequivocally related. The three species of sect. *Oreostemma* appear to be relatively homogeneous, the plants all with nine pairs of chromosomes, producing a taproot and short branched caudex, strictly monocephalous stems, stems and leaves eglandular or with few, short stipitate glands, entire, linear leaves with three parallel veins, and flattened pappus bristles. The phyllaries in subg. *Oreostemma* are slightly keeled but the midvein near the phyllary base is usually sunken rather than raised. None of these features except the chromosome number and taproot are matched in *A. kingii*.

On the other hand, *Aster kingii* clearly is similar in a suite of features to the group of species recently consolidated as the genus *Tonestus* A. Nels. (Nesom & Morgan 1990): habitats rocky and at high altitudes, plants rhizomatous or taprooted with ascending, woody caudex branches, leaves obovate, reticulate veined, and coarsely toothed, the basal persistent, the cauline continuing to immediately below the heads, outer phyllaries foliaceous, at least the inner with a raised keel beginning at the phyllary base and with distinctively extended, foliaceous apices, and achenes strigose, long, narrow, and multinerved, with a nearly symmetrical carpopodium and with a single series of pappus bristles terete to the very base and more or less even in length. The vestiture, particularly of the stems, is composed of very long (up to 0.7 mm), vitreous, biseriate, gland tipped trichomes (Type C trichomes, see Nesom 1976). Type

C trichomes are ubiquitous throughout the tribe, but such distinctively long ones are rare among American Astereae, where to my knowledge, outside of *Tonestus* they occur only in *Aster integrifolius* and *A. modestus* Lindl., *Xylorhiza wrightii* (A. Gray) E. Greene, and a few species of *Solidago* L. In other features, *A. integrifolius* is securely positioned within *Aster* but *A. modestus* is anomalous and more difficult to place; neither could be considered to be closely related to *Tonestus*. *Xylorhiza* is more similar to *Machaeranthera* Nees, and *Solidago* has been shown by DNA studies to be closely related to *Tonestus* (see Nesom *et al.* 1990 for a summary). Two species within *Tonestus* are atypical in their vestiture – *T. microcephalus* (Cronq.) Nesom & Morgan is glabrous to glabrate and *T. pygmaeus* (Torr. & Gray) A. Nels. usually is eglandular – but they belong in the genus on the basis of overall morphology. The type species, *T. lyallii* (A. Gray) A. Nels., which is apparently one of the most specialized in the genus with its calvous achenes and (at least in some plants) somewhat flattened pappus bristles, also produces the very long glandular trichomes.

Among the species of *Tonestus*, *T. aberrans* (A. Nels.) Nesom & Morgan is most similar to *Aster kingii*. Indeed, as a pair the two are somewhat set apart from the rest of the genus in their toothed leaves often with spinulose teeth, narrowly lanceolate-attenuate and apically spreading or reflexed phyllaries, style appendages with more widely arranged sweeping hairs, and purplish disc corolla lobes. *Tonestus aberrans*, however, has leaves more predominately cauline and consistently produces multi-headed capitulescences in contrast to the normally monocephalous stems of *A. kingii*, although the latter occasionally may produce up to five heads in a loose corymb (*vide* Welsh 1983). Further, the leaves of *T. aberrans* are glandular pubescent while those of *A. kingii* are glabrous or glabrate, and the phyllaries of *T. aberrans* are distinctly graduated in length, while those of *A. kingii* are somewhat variable in this respect but also tend to be graduated.

A conspicuous feature that has deterred consideration of *Aster kingii* as a member of any yellow rayed genus is its white ray color. The complete absence of rays, however, in three species of *Tonestus* (*T. aberrans*, *T. graniticus* [Tiehm & Shultz] Nesom & Morgan, and *T. alpinus* [Anderson & Goodrich] Nesom & Morgan) has not previously prevented botanists from recognizing their close relationship with the yellow rayed species (Anderson 1980; Tiehm & Shultz 1985). If the hypothesis of close relationship regarding *A. kingii* and *T. aberrans* is correct, the purplish pigments in the disc corolla lobes of *T. aberrans* are perhaps unmasked by a reduced amount of yellow pigment. *Tonestus graniticus* has strongly graduated phyllaries and is probably closely related to *T. aberrans*. On the basis of its broader phyllaries of nearly even length, *T. alpinus* is probably most closely related to *T. eximius* (H.M. Hall) A. Nels. & Macbr. and *T. peirsonii* (Keck) Nesom & Morgan.

A second disparity, at first sight, between *Aster kingii* and the species of *Tonestus* might be perceived in the relatively well defined taproot of the for-

mer. All but two species of *Tonestus*, however, produce woody, ascending caudex branches apparently arising from a single axis, although the latter is usually broken off of herbarium specimens, probably because of the difficulty in extracting them from their crevice habitats. *Tonestus pygmaeus*, however, is clearly taprooted with a multicapital crown and foreshortened caudex branches and is nearly identical in habit to *A. kingii*; *T. microcephalus*, and *T. peirsonii* are taprooted with longer caudex branches. The relatively slender, more diffuse rhizomes of *T. lyallii* and *T. eximius* do not arise from a central axis and in this respect are unusual in the genus. Within *Tonestus*, taproots have perhaps developed in the manner hypothesized by Welsh (1983), but a more detailed analysis of the generic phylogeny would be required to establish this with certainty. In any case, other genera of Astereae accommodate both taprooted and rhizomatous species (e.g., *Chrysopsis* [Nutt.] Ell., *Erigeron* L., *Grindelia* Willd., *Gutierrezia* Lag., *Machaeranthera* Nees, *Noticastrum* DC. and numerous others). Within *Aster*, *A. subulatus* Michx. of subg. *Oxytripolium* (DC.) Torr. & Gray is a taprooted annual, its closest relatives rhizomatous. The species of *Aster* subg. *Ianthe* (Torr. & Gray) A. Gray (or the genus *Ionactis* E. Greene) are variable in their production of short, woody rhizomes, caudex branches, and taproots (Nesom & Leary, submitted). The remaining species of *Aster* sensu lato are somewhat more uniform in their rhizomatous bases, although the cormoid rhizomes of subg. *Virgulus* (Raf.) A. Jones are distinctive.

In summary, *Aster kingii* shares with species of *Tonestus* a significant number of features, particularly including the distinctive vestiture of glandular trichomes with extremely long stipes. And in spite of its white rays, it fits more securely in that genus than in *Aster*, particularly when it is placed next to *T. aberrans*. This view of the taxonomic placement of *A. kingii* is reflected in the following two nomenclatural combinations:

Tonestus kingii (D.C. Eaton) Nesom, *comb. nov.* BASIONYM: *Aster kingii* D.C. Eaton, *Bot. Fortieth Parallel* 5:141. 1871. *Machaeranthera kingii* (D.C. Eaton) Cronquist & Keck, *Brittonia* 9:239. 1957.

Tonestus kingii (D.C. Eaton) Nesom var. ***barnebyana*** (Welsh & Goodrich) Nesom, *comb. nov.* BASIONYM: *Machaeranthera kingii* (D.C. Eaton) Cronquist & Keck var. *barnebyana* Welsh & Goodrich, *Brittonia* 33:299. 1981. *Aster kingii* D.C. Eaton var. *barnebyana* (Welsh & Goodrich) Welsh, *Great Basin Naturalist* 43:221. 1983.

Var. *barnebyana* is weakly distinguished, but it is restricted to the southwestern corner of the range of the species, and as noted in its original description, its leaves are characteristically toothed and the biseriate glands are longer than in the typical variety. In these features, var. *barnebyana* is more similar than var. *kingii* to related species within *Tonestus*.

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**TOMENTAURUM (ASTERACEAE: ASTEREA), A NEW GENUS OF
GOLDENASTER FROM CHIHUAHUA, MÉXICO**

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ABSTRACT

Tomentaurum, a new monotypic genus of the goldenaster lineage, is based on *Heterotheca vandevenderorum*, with the new combination **Tomentaurum vandevenderorum**. These plants are endemic to west central Chihuahua, México and are distinguished by the following combination of features: rhizomatous, leaves mostly basal, obovate-oblongate, dense and closely white tomentose, heads large, solitary, on long scapes, rays yellow and coiling, disc corollas very long, achenes narrowly oblong and strongly compressed, with numerous, whitish, superficial nerves, and pappus double. In its dense vestiture of minutely filiform hairs arising from similarly thin bases, *Tomentaurum* is hypothesized to be most closely related to the North American genera *Pityopsis* and *Croptilon*.

KEY WORDS: *Tomentaurum*, *Heterotheca*, *Pityopsis*, Astereae, Asteraceae, México

In a review and phylogenetic analysis (Nesom 1991a) of the genera closely related to the goldenasters *Heterotheca*, *Chrysopsis*, and *Pityopsis* (sensu Semple *et al.* 1980), it has become evident that a recently described species known by only a few collections from northwest México cannot be placed within any of the known goldenaster genera, although it is clearly a member of that phylad. Turner (1987) noted that the species was "very distinctive" but apart from placing it in *Heterotheca*, he did not offer an hypothesis regarding its possible closest relatives. The distinctive plants from Chihuahua are described here as a monotypic genus.

***Tomentaurum* Nesom, gen. nov.** Type species: *Heterotheca vandevederorum* B. Turner

Plantae rhizomatosae, folia praecipue basalia obovati-oblanco-lata dense arcte albo tomentosa, capitula grandia solitaria in scapis longis, corollae radii flavae circinnatae, corollae disci longae, achenia longae valde compressae nervis numerosis albidis superficialibusque, et pappus duplex.

***Tomentaurum vandevederorum* (B. Turner) Nesom, comb. nov.** BA-SYNONYM: *Heterotheca vandevederorum* B. Turner, *Phytologia* 63:127. 1987. TYPE: MÉXICO. Chihuahua: Río Mayo Region, El Capitán, 28° 13' 30" N, 108° 07' 30" W, 2000 m, 26 Jun 1986, *P.S. Martin* 56 (HOLOTYPE: TEX!; Isotype: ARIZ).

Perennial herbs from slender, slightly woody rhizomes, these producing long, caudexlike branches with scale leaves; stems, leaves, and phyllaries densely invested with short, biserial trichomes (Type C trichomes, see Nesom 1991a), each with a few celled, orange resinous head, the glands sometimes nearly sessile on the phyllaries, stems and leaves tomentose with very long, uniserial, few celled, minutely filiform white hairs from equally small bases (Type B trichomes), completely lacking coarser uniserial trichomes ("osteolate" or Type A trichomes). Stems unbranched, erect, stipitate glandular, closely tomentose. Leaves in a basal rosette or on the basal 3-10 cm of the stems, oblanceolate-obovate, 2-4 cm long, 3-9 mm wide, entire, the cauline subclasping, densely woolly tomentose, tardily glabrescent above. Heads 16-20 mm wide, solitary on scapose peduncles 12-25 cm long; receptacles very shallow convex, barely foveolate; phyllaries narrowly ovate-lanceolate, strongly graduated in 5-6 series, the inner 10-13 mm long, the margins purplish, with a prominent, scarious flange, the outer herbaceous, the middle strongly keeled, herbaceous only at the apex. Ray flowers 16-21, pistillate, fertile, yellow, 10-13 mm long, the ligules 2.0-2.5 mm wide, tightly coiling after receptivity of the ray stigmas. Disc corollas perfect, tubular, 8-9 mm long, the lobes with uniserial, acicular trichomes, with elongate, straight sided crystals in the tissues of the lower throat; style branches 1.4-1.7 mm long, with linear-lanceolate appendages 1/3-1/2 the length of the branches. Achenes densely white-sericeous, 4.5-5.5 mm long, 0.6-0.7 mm wide, strongly compressed, with 7-9 thin, closely adjacent, superficial, white nerves on each side, one or two of these often slightly thicker than the others; carpodium strongly asymmetric; pappus of 45-60 white, barbellate bristles in several series, with a few, inconspicuous setae or very slightly widened bristles 0.5-1.5 mm long. Chromosome number unknown.

Endemic to the plateau in the area of Basaseachic, Chihuahua; rocky stream beds or sandy-cobbly soil, area of pine woodlands; 2000-2100 m; flowering July-September.

Additional collections examined: MEXICO. Chihuahua: Rancho El Capitán, 28° 13' 30" N, 108° 07' 30" W, 22 Jun 1987, T.R. & R.K. Van Devender 87-134 with P. S. Martin (TEX); N edge of town of Basaseachic on Río de Basaseachic, 28° 12' 40" N, 108° 12' 50" W, 24 Jun 1987, T.R. & R.K. Van Devender 87-165 with P. S. Martin (TEX).

Tomentaurum is a member of the goldenaster lineage (Nesom 1991a), as evidenced by its stipitate glandular herbage, keeled phyllaries, ray flowers with yellow, coiling ligules, disc corolla throats with elongate crystals, linear-lanceolate disc style appendages, achenes with asymmetric carpodia, and the pappus with an outer series of members much shorter than the inner. The narrow achenes with numerous, superficial nerves appear to be of relatively primitive morphology (Nesom 1991a).

Plants of *Tomentaurum* are habitally distinctive: they are rhizomatous, the rosettes arising from somewhat herbaceous, slender caudex branches with scale leaves, the basal leaves persistent, obovate-oblongate, densely and closely white tomentose, and the scapose stems long and unbranched, bearing large, solitary heads. The only goldenaster species that are somewhat similar in habit (i.e., rhizomatous, basal leaves persistent, monocephalous) are *Heterotheca chihuahuana* (Turner & Sundberg) B. Turner and those of *Osbertia* E. Greene and *Noticastrum* DC. (Nesom 1991b), but all of these differ strongly from *Tomentaurum* in significant features (Nesom 1991a).

In its dense tomentum of highly elaborated, minutely filiform hairs arising from similarly thin bases (Type B trichomes; see Nesom 1991a for trichome terminology), *Tomentaurum* is hypothesized to be closely related to the North American genera *Pityopsis* Nutt. and *Croptilon* Rafin. (Nesom 1991a). *Tomentaurum* differs from both of the latter genera, particularly in its less specialized leaves (shape, venation, and anatomy), glandular trichomes with much less highly elaborated heads, large, solitary capitula, and strongly compressed achenes. All species of *Heterotheca* (except *H. chihuahuana* and *H. mucronata* Harms ex Turner) are taprooted and produce relatively short, thick walled Type A trichomes mixed with an understory of minute, inconspicuous Type B trichomes.

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TRANSFER OF *HETEROTHECA BARTLETTII* TO *OSBERTIA*
(ASTERACEAE: ASTEREAE)

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ABSTRACT

Heterotheca bartlettii, endemic to Tamaulipas and Nuevo León, México, is transferred to the genus *Osbertia*. The latter has been monotypic for most of its taxonomic history, with the exception of one species recently added to it but subsequently transferred to *Heterotheca*. With the addition of *O. bartlettii*, *comb. nov.*, *Osbertia* again becomes di-
typic.

KEY WORDS: *Osbertia*, *Heterotheca*, *Haplopappus*, Asteraceae, Astereae, México

In the process of preparing a taxonomic treatment of the Mexican genera of goldenasters for the "Asteraceae of México" (Turner & Nesom, in prep.) as well as a phylogenetic analysis of the whole goldenaster lineage (Nesom 1991), it has become apparent that *Heterotheca bartlettii* (S.F. Blake) M.C. Johnston (= *Aplopappus bartlettii* S.F. Blake) is in need of taxonomic realignment.

In the original description of (*H*)*Aplopappus bartlettii*, Blake noted that the uniseriate pappus was the single feature that argued for the placement of the species in *Haplopappus* DC. rather than *Chrysopsis* (Nutt.) Ell. He referred the species to *Haplopappus* sect. *Isopappus* (Torr. & Gray) Hall (= *Croptilon* Rafin.), but it is not clear why he did not ally it instead with *Haplopappus* sect. *Osbertia* (DC.) Hall, because he recognized the large difference between *H. bartlettii* and the species of sect. *Isopappus*. Johnston transferred the species to *Heterotheca* Cass., positioning it with phylogenetically close relatives, including some species in which the outer pappus is obscure. Smith (1965) agreed in excluding *Haplopappus bartlettii* from sect. *Isopappus*, accepting its placement in *Heterotheca* pending further study.

Turner & Sundberg (1986) did not mention *Heterotheca bartlettii* in their formal treatment of *Osbertia* DC. They did, however, add a second species, *O. chihuahuana* Turner & Sundberg, to the single original one, *O. stolonifera*

(DC.) E. Greene. In a re-examination of *O. chihuahuana*, Turner (1987) has transferred it to *Heterotheca*, where although it is still somewhat anomalous in habit, it is more naturally situated in its overall combination of characters, particularly in its vestiture.

On the other hand, *Heterotheca bartlettii* differs from *Heterotheca* (including sects. *Heterotheca*, *Phyllothea* [Nutt.] Harms, and *Ammodia* [Nutt.] Harms) and all of the other genera of the goldenaster lineage in a combination of characters that in turn match those in *Osbertia stolonifera*: uniseriate, long, thin walled, and vitreous trichomes (Type A trichomes, see Nesom 1991a for terminology), herbaceous phyllaries without an indurated keel, reddish tinged ray flowers with noncoiling ligules, subterete, nearly cylindric achenes with numerous, superficial nerves, and a simple pappus. The achenes of *Osbertia*, with numerous, superficial nerves, are primitive within the goldenaster lineage. The simple pappus and the herbaceous, nearly unkeeled phyllaries are found only in *Osbertia*, but several features of *O. stolonifera* and *H. bartlettii* are shared with species of two closely related genera (Nesom 1991b): the distinctive Type A trichomes occur in the South American genus *Noticastrum* DC. and in all species of *Chrysopsis*; noncoiling ray ligules are found in *Noticastrum* as well as a pair of species of *Chrysopsis*; reddish pigments in the ray corollas occur in *Osbertia* and *Noticastrum*.

An additional similarity between *Osbertia stolonifera* and *Heterotheca bartlettii* is found in their disc corollas, which in both species produce elongated crystals from the very base of the tube to the lower throat; stellate "sand" crystals are not produced at all. The disc corollas of all other genera of the goldenaster lineage typically (and diagnostically) produce elongated crystals (Nesom 1991a), but only in *Osbertia* are "sand" crystals completely lacking.

The chromosome number of *Osbertia stolonifera* has been reported as $n = 5$ pairs (commonly) and $n = 4$ pairs (rarely) (see Turner & Sundberg 1986, for numerous records); no chromosome count is available for *Heterotheca bartlettii*, but this information will be significant in further substantiating the comparison between the two species.

In summary, *Heterotheca bartlettii* is such a close morphological match for *Osbertia stolonifera* that the two are best placed in the same genus.

Osbertia bartlettii (S.F. Blake) Nesom, *comb. nov.* BASIONYM: *Aplopappus bartlettii* S.F. Blake, J. Washington Acad. Sci. 22:328. 1932. TYPE: MÉXICO. Tamaulipas: Above La Vagonia near San Jose, 1100 m, 3 Jul 1930, *Bartlett 10046* (HOLOTYPE: MICH; Isotype: US!). *Heterotheca bartlettii* (S.F. Blake) M.C. Johnston, Southw. Nat. 2:172. 1958.

Perennial herbs from slender, woody rhizomes, the stems, leaves, and phyllaries prominently invested with long, stipitate glandular hairs, also sparsely and closely villous-puberulent with minute, nonglandular hairs, sparsely long

pilose with vitreous, sometimes flattened and twisted trichomes (Type A) arising from thin bases. Stems 8-25 cm tall, often scapose when the cauline leaves strongly reduced. Basal leaves oblanceolate, persistent, the cauline with sub-clasping bases, when present restricted to the lower third of the stem. Heads 7-10 mm wide, usually solitary on long, naked peduncles 3-10 cm long; receptacles smooth or very slightly foveolate; phyllaries linear-lanceolate, 1 nerved, the nerve sometimes orangish, not keeled, with a herbaceous midregion and indurated margins from base to tip, strongly graduated. Ray flowers 23-33, the corollas 8-10 mm long, usually drying with an abaxial, purplish midstripe, not coiling. Disc corollas 4.0-4.5 mm long, the lobes minutely viscid glandular; style appendages linear-lanceolate, 0.6-0.8 mm long, 1/3-1/2 the length of the style branches. Achenes sparsely short strigose, cylindric, terete to slightly compressed, with ca. 16, slender, evenly spaced, superficial nerves; carpodium asymmetric; pappus of ray and disc achenes uniseriate, of 15-20 barbellate bristles, without an outer series.

Nuevo León and Tamaulipas, México; meadows or openings, oak, oak-pine, or pine woodlands, 900-1800 m; flowering July to September.

Additional collections examined: MÉXICO. Nuevo León: Dulces Nombres, and just E of border into Tamaulipas, 20 Jul 1948, *Meyer & Rogers 2827* (MO); Mpio. Villa Santiago, Cañon Denuncio, Rancho La Bolla, upper canyon, 22 Jun 1935, *Mueller 2008* (MO); Mpio. Villa Santiago, trail between Potrero Redondo and Laguna Sanchez, 16 Aug 1939, *Mueller 2721* (MO); Mpio. Montemorelos, La Trinidad, 19 Aug 1939, *Muller 2854* (LL). Tamaulipas: Sierra de San Carlos, Cerro El Diente, 7 Jun 1985, *Jiménez 268* (TEX); road from Vicente Guerrero toward El Molino, 30 km W of Victoria, 23 Sep 1985, *Yanez 547* (TEX); Sierra de San Carlos, 5 mi S of San Carlos, N side of Bufo El Diente, 15 Apr 1988, *Nesom 6296* (MEXU, TEX).

Standley marked collections of *Mueller 2008* (cited above) as the type of a species of *Chrysopsis*, using the epithet "longipes," but this name apparently was never published.

Osbertia is most closely related to the genera *Chrysopsis* of the eastern and south central United States and *Noticastrum* of South America (Nesom 1991a, 1991b). The two species of *Osbertia* are restricted primarily to eastern México and northern Central America, where they have allopatric, nearly contiguous geographic ranges. They can be distinguished by the following contrasts:

1. Plants with short, thick rhizomes and leafy runners producing terminal plantlets; heads 16-30 mm wide; ray flowers 34-150, 15-25 mm long; southern Nuevo León to Guatemala. *O. stolonifera*
1. Plants with slender, woody rhizomes, without runners; heads 7-10 mm wide; ray flowers 23-33, 8-10 mm long; west-central Tamaulipas and adjacent Nuevo León. *O. bartlettii*

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A PHYLOGENETIC HYPOTHESIS FOR THE GOLDENASTERS (ASTERACEAE: ASTEREAE)

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ABSTRACT

The seven genera of the goldenaster lineage are included in a phylogenetic analysis based primarily on morphological data. They are hypothesized to form three separate clades: (1) *Chrysopsis* (including *Bradburia*), *Osbertia*, and *Noticastrum*, (2) *Croptilon* and *Pityopsis*, which are sister genera, and *Tomentaurum*, and (3) *Heterotheca* (including sects. *Ammodia*, *Heterotheca*, and *Phyllothea*). The genus most closely related to the goldenaster lineage is taken to be *Ionactis* (= *Aster* sect. *Ianthe*).

KEY WORDS: *Heterotheca*, *Ionactis*, *Aster*, Asteraceae, Astereae

Recent studies of restriction site variation in chloroplast DNA of North American Astereae (Suh 1989; Morgan 1990) have produced a relatively clear delimitation of a phyletically coherent group of genera termed the "goldenasters." Suh's sample included *Croptilon* Rafin., *Pityopsis* Nutt., *Heterotheca* Cass. (sect. *Heterotheca*), *Bradburia* Torr. & Gray, and *Chrysopsis* (Nutt.) Ell.; Morgan's sample included *Croptilon* and *Osbertia* E. Greene. Semple *et al.* (1980) postulated that *Chrysopsis* and *Bradburia* are part of an evolutionary lineage completely apart from the others, but for the most part, recent treatments have recognized the goldenaster genera as a natural group, at least implicitly, since many authors have viewed *Chrysopsis*, *Pityopsis*, and *Heterotheca* (including sects. *Heterotheca*, *Phyllothea* [Nutt.] Harms, and *Ammodia* [Nutt.] Harms) in various combinations as only one or two genera (see Semple 1977 for a review). The studies of Semple and colleagues have been instrumental in illuminating the distinctions among these taxa (see Semple *et al.* 1980 for a review and overview) and have provided separate taxonomic studies of *Chrysopsis* (Semple 1981), *Pityopsis* (Semple & Bowers 1985), *Heterotheca* sect. *Ammodia* (Semple 1988), and *Bradburia* (Semple & Chinnappa 1984). Other of the genera have also been the subjects of relatively recent taxonomic

treatments (*Croptilon*, Smith 1966, 1981; *Osbertia*, Turner & Sundberg 1986, Nesom 1991a; *Heterotheca* sect. *Heterotheca*, Nesom 1990), and Nesom (1991c) has presented evidence for uniting the monotypic *Bradburia* with *Chrysopsis* in a phylogenetic analysis of the latter.

In addition to the genera above, Turner & Sundberg (1986) noted that the South American genus *Noticastrum* DC. (see Cuatrecasas 1973; Zardini 1978) probably should be included as a member of the goldenaster lineage, and evidence from the present study supports its inclusion. *Tomentaurum* Nesom, a newly described monotypic genus from western Mexico has been added to the goldenasters (Nesom 1991b).

There is further indication, based on the cpDNA studies of Suh (1989) and Morgan (1990), that the white rayed *Boltonia* L'Herit. and *Chloracantha* Nesom *et al.* are more closely related to the goldenasters than to any other species in their studies, although they are highly divergent in morphology and appear to be weakly associated somewhere at the very base of the phylad (Nesom *et al.* 1991). They are not included in the present analysis.

The molecular studies of Suh & Morgan placed the goldenaster lineage most closely to the *Machaeranthera* Nees and *Aster* L. lineages (see Nesom *et al.* 1989, for a summary). Neither of their studies, however, included a wide range of species traditionally accommodated in *Aster*. A morphologically based phylogenetic overview of *Aster* and related genera (Nesom in prep.) hypothesizes that the taxa most similar to the goldenasters lie among the groups of *Aster* not included in the recent molecular analyses, those with carinate phyllaries, a double pappus, and a base chromosome number of $x = 9$. Among these, *Aster* subg. *Ianthe* [Torr. & Gray] A. Gray, with strongly asymmetric carpopodia, is hypothesized to be the sister group to the goldenasters. Additional comments are provided by Nesom & Leary (submitted), who treat the group at generic rank as *Ionactis* E. Greene and add a fourth species to it.

The studies noted above have offered various ideas regarding relationships of genera within the goldenaster group, but none have included all of the taxa involved. The present study confirms the evolutionary unity of the seven genera of goldenasters on a morphological basis and provides a phylogenetic hypothesis for all of them.

CLADISTIC ANALYSIS - METHODS

Studies of microcharacters were made with a compound microscope. Glands, trichomes, foliar veins were studied from epidermal "skims" and cross sections made with a razor from stems and leaves; these and dissected flowers have been mounted on slides in Hoyer's Medium. A list of specimens from which slides have been made is deposited at TEX; all voucher specimens are deposited in TEX. Characters and character states used in the analysis are given in Table

1; coding for the individual taxa are in Table 2; discussion of variability in the characters is provided in the Appendix. The data were analyzed using PAUP (Swofford 1985) with Wagner parsimony.

Some decisions regarding evolutionarily primitive character states in *Chrysopsis*, which comprises two sharply disparate sections, have been made in a separate analysis (Nesom 1991c). Section *Phyllothea* of *Heterotheca* is a variable group and is represented in the present analysis by two species, *H. mexicana* Harms ex B. Turner and *H. stenophylla* (A. Gray) Shinnners, these chosen to broaden the variability included in the character scoring. The genus *Ionactis* serves as the outgroup in the present analysis, since it appears to be the group most closely similar and probably most closely related to the goldenasters.

RESULTS and DISCUSSION

The goldenaster lineage is characterized by a number of morphological features, some shared with related groups and some that distinguish it from the *Aster* and *Machaeranthera* lineages: stipitate glandular herbage, carinate phyllaries, yellow ray flowers, throat tissues of disc corollas with numerous, straight sided, elongate crystals, disc style branches have linear-lanceolate appendages, multinerved achenes, asymmetric carpopodia, and pappus of slender, basally terete bristles with a much shorter outer series. In *Heterotheca* and *Chrysopsis*, the heads are borne in a corymboid cyme arising from the distal portion of the main branches, with a tendency to be somewhat more loosely arranged in *Pityopsis* and *Croptilon*. Further, it seems clear that the base chromosome number for the group is $x = 9$. Of particular significance in this study has been the discovery that the goldenaster genera appear to stand apart from almost all other North American Astereae in their production of long, straight sided crystals in the tissues of the disc corolla throats. Similar crystals have been observed elsewhere only in *Xylorhiza* Nutt., *Grindelia* Willd., and *Prionopsis* Nutt. (Nesom *et al.* submitted), which are related to *Machaeranthera* rather than the goldenasters (Morgan 1990). Further details regarding these crystals are provided in the Appendix.

A single tree of 36 steps (Fig. 1) accounts for the distribution of character states scored in the present analysis. Three primary lineages are defined, referred to here as the *Chrysopsis*, *Heterotheca*, and *Pityopsis* lineages, since the present study fully corroborates the earlier conclusion by Semple *et al.* (1980) that each of these three genera is phyletically distinct from the other two. The single character (no. 18, vestiture of the disc corolla lobes) that unites the *Heterotheca* and *Pityopsis* lineages is the most homoplasious of all those in the present study, and it must be viewed as nearly weightless evidence in resolving what otherwise would be a basal trichotomy. If it were assumed

TABLE 1. Characters and character states.

-
1. Chromosome number, (0) $x = 9$ or 7 (1) $x = 5$ or 4
 2. Taproot or rhizomes, (0) rhizomes (1) taproot
 3. Leaf shape and venation pattern, (0) obovate to oblanceolate, net veined (1) linear, parallel veined or with a strong tendency for parallel veins
 4. Leaf venation/anatomy, (0) veins not strongly sclerenchymatous, not raised above the lamina (1) veins with associated massive sclerenchyma, prominently superficial and forming ridges,
 5. Biseriate (Type C) trichomes, (0) without a differentiated head or the head merely 2 celled, the only form of Type C trichomes present (1) at least some with a highly elaborated head 4-8 cells wide at the apex, on a distinct stalk
 6. Type A trichomes on herbage, (0) abundant (1) few in number or completely absent
 7. Type A trichomes, (0) thick-walled, terete, or absent (1) thin walled, often flattened and twisted
 8. Type A trichomes - outer walls, (0) smooth or absent (1) papillate
 9. Type B trichomes, (0) minute, less than 0.5 mm long (1) filamentous, highly elaborated in length, sometimes forming a dense, close, tomentum
 10. Head arrangement, (0) numerous in a corymboid cyme arising from branches on the upper third of the primary stem (1) solitary on moncephalous stems
 11. Head width, (0) mostly (8-)10-20 mm (1) mostly 4-7 mm
 12. Phyllary morphology, (0) indurated at least basally, with a narrow, raised, white indurated keel (1) herbaceous throughout, or at least the medial nerve not at all keeled
 13. Ray corolla color, (0) bluish (1) yellow
 14. Ray corolla color, (0) bluish or yellow (1) yellow, tinged with reddish purple
 15. Ray corolla behavior after stigma receptivity, (0) coiling (1) remaining straight

TABLE 1. (continued).

16. Cells of disc corolla throat, (0) with stellate "sand" crystals or without crystals (1) with elongate, straight sided crystals
 17. Radial wall of cells of disc corolla throat, (0) broadly sinuate (1) straight
 18. Disc corolla lobes, vestiture (0) glabrous or with biseriate, glandular hairs (1) with uniseriate, acicular hairs, commonly also with obscure glandular hairs
 19. Vascular bundles in collecting appendages of disc flower style branches, (0) unsclerified (1) sclerified
 20. Disc achene surface, (0) with nerves subepidermal or raised but not resinous (1) with numerous, thin, slightly resinous nerves flush with surface
 21. Disc achene surface, (0) with (2-)8-26 thin, superficial, nerves, or the nerves not thick and rounded (1) with thick, rounded ridges, the nerves completely below the epidermal surface
 22. Disc achene nervation, (0) (6-)8-26 nerved (1) 2-(3-6) nerved
 23. Achene shape, side view, (0) narrowly oblong to oblong elliptic, symmetric (1) obovate, asymmetric
 24. Disc achene shape, (0) distinctly compressed (1) terete or subterete
 25. Pappus series, (0) double, the outer much shorter than the inner and varying from setae to linear scales (1) single, of bristles relatively even in length
 26. Pappus bristle shape in cross section, (0) terete (1) flattened
-

TABLE 2. Data matrix for the goldenaster taxa analyzed.

Taxa	Character State					
<i>Ionactis</i> (IONACT)	00000	00000	00000	00000	00000	0
Sect. <i>Ammodia</i> (AMMODI)	01001	00100	00100	11110	01000	1
<i>Heterotheca mexicana</i> (HMEXIC)	01001	00100	00100	11111	01000	1
Sect. <i>Heterotheca</i> (HETERO)	01001	00100	00100	11011	01100	1
<i>Heterotheca stenophylla</i> (HSTENO)	01001	00100	00100	11011	01000	1
<i>Tomentaurum</i> (TOMENT)	?0001	10011	00100	11110	01000	0
<i>Pityopsis</i> (PITYOP)	00111	10010	10100	11110	01010	0
<i>Croptilon</i> (CROPTI)	01111	10010	10100	11010	01011	0
<i>Noticastrum</i> (NOTICA)	0?001	01001	00111	11110	01000	0
<i>Osbertia</i> (OSBERT)	10001	01001	01111	10010	01011	0
<i>Chrysopsis</i> (CHRYSO)	10001	01000	00100	11010	11100	0

that the Type A trichomes were present in the goldenaster ancestor and lost twice in the *Chrysopsis* lineage, the trichotomy would remain unresolved with the addition of a single additional step in the same character.

Each of the three goldenaster lineages is distinguished primarily by the nature of its vestiture (see Nesom 1976 and further comments in the Appendix). All of the goldenaster taxa usually have stipitate glandular hairs, but those of the *Chrysopsis* lineage are characterized by their relatively long Type A trichomes with thin, smooth walls, those of the *Heterotheca* lineage by Type A trichomes with papillate outer walls, and those of the *Pityopsis* lineage by the absence or near absence of Type A trichomes and the presence instead of greatly lengthened and prominent Type B trichomes.

Apart from the relationship of the three primary lineages, the goldenaster phylogeny appears to be relatively well resolved, based on the data available, but several other problematic and unsatisfying points remain. First, the placement of *Osbertia* and *Chrysopsis* as sister species, rather than *Osbertia* and *Noticastrum*, would be more consistent with a well known geographic pattern of diversification, where closely related taxa occur both in the southwestern United States and in eastern Mexico, and it would not require a parallel reduction in chromosome number from $x = 9$ to $x = 5$. A study of the $x = 5$ *Chrysopsis* and $x = 5$ *Osbertia* karyotypes might prove to be critical in this interpretation. Second, *Tomentaurum* is so very different from *Pityopsis* and *Croptilon* in habit, leaf morphology, and other features, as well as different from the probable ancestor to the whole goldenaster phylad, that it would not be surprising if it were placed, on the basis of additional evidence, closer to any of the other genera. Finally, *Heterotheca* (sensu Semple *et al.* 1980 and the

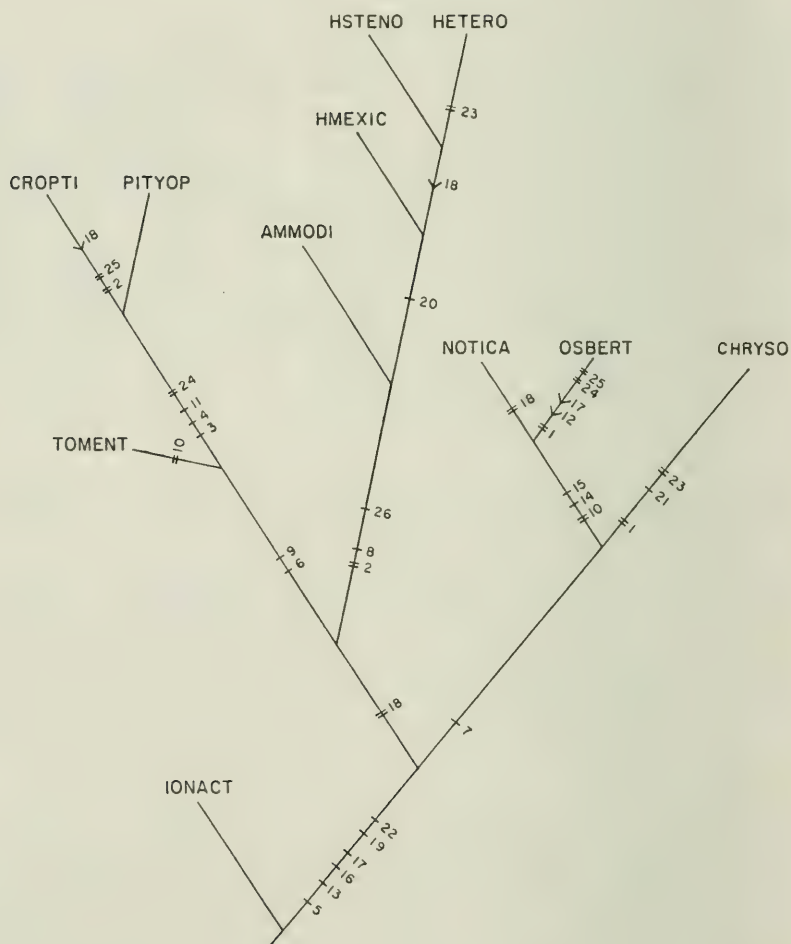


Figure 1. Phylogenetic reconstruction of the goldenaster lineage. Abbreviations for the taxa follow those in Table 2. Single slash = apomorphy or autapomorphy; double slash = parallelism; downward arrow = reversal.

present analysis) can be maintained as a single genus, but sect. *Phyllothea* probably is paraphyletic and better treated as several separate sections (the data of this analysis do not show this as clearly as possible). Alternatively, the monotypic *Heterotheca* sect. *Ammodia* (*H. oregona* [Nutt.] Shinners) might justifiably be segregated as a monotypic genus, as did Nuttall originally.

The cladistic topology postulated here, based on morphology, differs slightly from a relatively unresolved cladogram based on molecular data (Suh 1989), although the latter analysis included only four of the taxa treated here. Suh positioned *Heterotheca* sect. *Heterotheca*, *Pityopsis*, and *Croptilon* as a trichotomy that is phyletically coordinate with the species pair *Chrysopsis pilosa* Nutt. and *C. texana* Nesom (= *Bradburia*). Both of the latter two are treated by Nesom (1991c) as *Chrysopsis* sect. *Bradburia* (Torr. & Gray) Nesom. Morgan's analysis (1990) included only two goldenaster genera and placed *Osbertia* coordinate with several species of *Croptilon*.

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APPENDIX 1. Notes on character variation

1. The ancestral chromosome number for the *Heterotheca* lineage appears to be $x = 9$, based on the hypothesis that *Noticastrum* is closely related to *Osbertia* and *Chrysopsis* (Nesom 1991c), as well as on the taxa presumably most closely related to the goldenasters, including *Ionactis* and others (Nesom in prep.). The species of *Croptilon* have an aneuploid series of $n = 7$, $n = 6$, $n = 5$, and $n = 4$; the genus is scored with the $x = 9$ taxa, based on evidence presented by Smith (1966), who showed that the lower numbers within *Croptilon* are derived sequentially from the higher. Although no populations with $n = 8$ or $n = 9$ have been discovered, it is probable and assumed here that $n = 7$ in *Croptilon* has also been derived from a base of $x = 9$.

2. *Noticastrum* comprises both rhizomatous and taprooted species and it has been scored ambiguously. All species of *Heterotheca* are taprooted, except the rhizomatous *H. chihuahuana* (Turner & Sundberg) B. Turner and *C. mucronata* Harms ex Turner, which apparently are derived from taprooted ancestors. Plants of a previously undescribed species of *Ionactis* produce a taproot, but this is also apparently evolutionarily derived from the short, woody rhizomes of the other species (Nesom & Leary submitted).

3 and 4. *Pityopsis* and *Croptilon* stand alone among the other genera in their linear or narrowly oblong leaves with acute apices. The major foliar veins of *Pityopsis* are strictly parallel; the veins of *Croptilon* show a strong tendency to run parallel, usually with a single pair of laterals continuous from base to apex. And in contrast to the other genera, the foliar veins of both *Pityopsis* and *Croptilon* have large masses of associated sclerenchyma. Another distinctive feature of *Pityopsis* illustrated by Semple *et al.* (1980), the "sunken" abaxial epidermis, is present and even more pronounced in *Croptilon*, where it could be described as "lacunate."

5-9. Trichome terminology follows the designations in Nesom (1976), based on a study by Drury & Watson (1966). Type A trichomes have also referred to as "osteolate" (Semple *et al.* 1980) or as "helianthoid;" these are uniseriate and have thick, often roughened walls and the bases commonly are multicellular. Type B trichomes are also uniseriate but have thin, single celled bases and much thinner walls; in most taxa they are much smaller than the Type A trichomes, although in some of the goldenaster genera, they have supplanted the Type A trichomes and are the largest and most prominent. Type C trichomes are biseriate, usually with thin walled cells, and they typically are glandular in appearance. The simplest form has no head, with apical cells similar to the stalk cells - these are rarely found on herbage in the goldenaster group but elongated ones typically occur on the tubes of both ray and disc corollas. In the goldenasters, the apical cells are usually numerous and massed into a distinct, glandular head (3-8 cells wide at the apex) at the end of a stalk,

which is often long but variable in length among species. In these capitate trichomes, a droplet of transparent, yellow-orange resin may be formed at the tip of the head, and a membrane sometimes seems to enclose the droplet. Stages in the ontogeny of Type C trichomes have been documented and illustrated by Carlquist (1961).

Within *Noticastrum*, *N. hatschbachii* Zardini produces large glands; in the other species, Type C trichomes are present but unelaborated from the primitive biseriate, noncapitate form. Similar variation is present within *Heterotheca* sect. *Phyllotheca*. Various species within *Croptilon*, *Pityopsis*, and *Chrysopsis* usually lack Type C trichomes, but this is clearly a derived condition. In *Heterotheca* sect. *Ammodia*, there appear to be two distinct size classes of Type C trichomes, undifferentiated ones and large headed ones on thick stalks, although it is possible that these may simply represent ontogenetic stages.

In the tribe Astereae, Type A, B, and C or modifications of these appear to be the only kinds of trichomes present on the herbage. Homologies among trichome types can be established by examining the array of types present on a single plant. If only one of the uniseriate types is present, wall thickness and the nature of the trichome base are usually sufficient to distinguish it. The achene surfaces typically produce a second type of biseriate hair, the Zwillingshaare, which are ubiquitous throughout the tribe. Zwillingshaare rarely are produced on corollas, but they are primarily restricted to the achenes and have not been given an equivalent "Type" designation.

Type A trichomes are present in most species of all genera involved in the present analysis except *Pityopsis* and *Tomentaurum*, where they are completely absent. They are greatly reduced in number in *Croptilon*, where they are found primarily as spreading cilia along the petiolar margins. In *Osbertia*, *Chrysopsis*, and *Noticastrum*, Type A trichomes have thin, smooth, and vitreous walls, and they are commonly flattened and longitudinally twisted. In many taxa of *Chrysopsis* and *Noticastrum* they are distally elongated into fine, flexuous, flagelliform hairs. In the remainder of the goldenaster genera, the Type A trichomes are terete and have thicker walls. Semple et al. (1980) have shown that such trichomes in *Heterotheca* (including sects. *Heterotheca*, *Phyllotheca*, and *Ammodia*) have minutely papillate cell surfaces. Such surfaces apparently do not occur in other taxa of the goldenaster lineage, judging from studies with the compound microscope. *Heterotheca inuloides* Cass. produces vitreous trichomes similar to those in *Chrysopsis*, but they still have slightly papillate surfaces and certainly have developed their characteristics independently of those in the *Chrysopsis* lineage. In plants of *Heterotheca* the Type A trichomes often appear to be highly variable in length, even perhaps grading into Type B trichomes. Comparative data in greater detail (SEM) would be helpful for these taxa.

Type B trichomes are present in the goldenasters in their primitive form as thin walled, uniseriate hairs at least an order of magnitude smaller than

the Type A trichomes, except in the *Pityopsis* lineage, where they appear in several modifications. In *Pityopsis* and *Tomentaurum*, they are minutely and evenly filiform, forming a dense, close tomentum; they are parallel and sometimes anastomosing in *Pityopsis* but irregularly oriented and matted in *Tomentaurum*. In *Croptilon*, conspicuously lengthened Type B trichomes are apparent only on the abaxial surface of some species, where they originate in the "lacunae." On some plants of *C. divaricatum* (Nutt.) Rafn., these are dense enough to form a thin but conspicuous tomentum over the leaf surface. Some taxa of *Croptilon* and *Pityopsis* are glabrous or nearly so, lacking all trichomes.

10. Plants of *Tomentaurum* produce strictly monocephalous stems; those of *Osbertia* are mostly monocephalous, but the primary stems of *O. bartlettii* (S.F. Blake) Nesom produce a few lateral branches. Most species of *Noticastrum* are monocephalous, and *Heterotheca chihuahuana* is the only monocephalous species of its genus. It seems clear that monocephaly is a derived feature in the goldenasters, having arisen independently in several lineages.

11. The heads of *Croptilon* and *Pityopsis* are distinctly smaller than those of the other genera. Further, they are longer than wide, appearing cylindric, in contrast to those in the rest of the goldenasters, which are about as long as wide. The heads of *Chrysopsis texana* (= *Bradburia*) are exceptionally small, but this certainly has resulted from the sterility of the disc flowers. Among the species of *Ionactis*, the heads of *I. cieloatica* are also small (Nesom & Leary submitted) and are reduced independently of the small ones among the goldenasters.

12. Keeled phyllaries are one of the conspicuous features of the goldenaster group, although they are also characteristic of related genera (Nesom in prep.). At least on the basal portion of the phyllary, the medial nerve is indurated, not at all resinous, and sharply and narrowly raised. The medial nerve in phyllaries of *Croptilon*, and in some *Pityopsis*, is sometimes resinous from base to tip, lacking an indurated covering, but some taxa have a clearly discernible keel with a morphology that is similar to the other genera. The orange nerves in *Osbertia* also are sometimes exposed, and among the goldenasters, only its two species have completely herbaceous phyllaries without a distinct keel, although they are approached by some in *Chrysopsis*. The medial nerve in the phyllaries of *Noticastrum* is keeled, but at least in the inner phyllaries there are usually an additional 1 or 2 pairs of smaller, unraised nerves conspicuously present on either side of the medial one.

13 and 14. In a phylogenetic overview of *Aster* and related groups (Nesom in prep.), the blue rayed genus *Ionactis* is the sister group of the yellow rayed genera of goldenasters. Ray color variation in *Noticastrum*, where white rays apparently are derived from yellow ones, is discussed in more detail in another paper (Nesom 1991c).

The primarily yellow rayed *Machaeranthera* alliance also appears to be

closely related the *Aster* group, based on molecular data of Suh (1989) and Morgan (1990). Only two genera within it have white or blue rayed taxa: *Machaeranthera* (sensu Hartman 1990), which comprises both yellow and white or blue rayed species, and *Xylorhiza*, where all taxa are white or blue rayed. Morgan's molecular data show *Xylorhiza* to be the most primitive genus in the *Machaeranthera* lineage, its position there analogous to that hypothesized for *Ionactis* in the goldenaster lineage. Both yellow and white rayed species are hypothesized to occur within the genus *Tonestus* A. Nels. (Nesom 1991d) as well as among genera related to *Gutierrezia* Lag. (Nesom in prep.).

15. The corollas of postreceptive ray flowers in most genera of the goldenaster lineage coil tightly inward, with the adaxial surface exposed. However, they remain straight in *Noticastrum* and *Osbertia*, as well as in two species of *Chrysopsis*, where that behavior is hypothesized to have arisen in parallel with the former two genera (Nesom 1991c). Coiling ray corollas occur in most of North American Astereae, including the *Aster* and the *Machaeranthera* lineages. Ray corollas in *Erigeron* L., however, display a number of different behaviors, although for the most part the behavior appears to be consistent among species of a single section (Nesom 1989). Further aspects of variation in ligule behavior in the family are noted by Stirton (1983).

16. The difference between sinuate and straight walls can be easily seen in the cells of the upper throat of the disc corollas. Sinuate walls are particularly characteristic of the disc corolla throats in some groups of *Aster* as well as related genera but not in the goldenasters.

17. Relatively large, elongate, straight sided crystals are found in the throat cells of all species of species of goldenaster except *Chrysopsis texana*. Straight sided crystals much reduced in size occur in *C. pilosa*. The occurrence of these crystals appears to be one of the most significant diagnostic features of the goldenaster lineage, and their absence or reduction in two taxa clearly within the lineage on the basis of other characters is interpreted as apomorphic. The disc corolla tubes usually produce stellate "sand" crystals, and the transition between the large crystals of the throat and the much smaller "sand" crystals of the tube is abrupt. The disc corollas of *C. texana* produce only "sand" crystals. Both species of *Osbertia* produce only straight sided crystals in the disc corollas, from the base of the tube into the throat.

In a survey of disc corolla morphology of other genera of American Astereae, crystals similar to those in the goldenasters have been observed (Nesom *et al.* submitted) only in the genus *Xylorhiza* (8 species examined), *Grindelia* (8 species examined), *Prionopsis* Nutt., and *Hazardia* E. Greene (4 species examined), where they are highly reduced in size. The following genera have been examined and found to produce only "sand" crystals (number of species studied in parenthesis, if more than one): *Aphanostephus* DC., *Aster* sensu lato (18), *Baccharis* L., *Boltonia* L'Herit., *Chaetopappa* DC., *Chloracantha* Nesom *et al.*, *Corethrogyne* DC., *Ericameria* Nutt., *Erigeron* (11), *Euthamia* Nutt.,

Gutierrezia, *Gymnosperma* Less., *Haplopappus* DC. (3 South American), *Hysterionica* Willd., *Isocoma* Nutt., *Machaeranthera* (8), *Monoptilon* Torr. & Gray, *Olivaea* Sch.-Bip. ex Benth., *Oonopsis* E. Greene (2), *Oritrophium* (Kunth) Cabr., *Petradoria* E. Greene, *Pyrocoma* Hook., *Solidago* L. (3), *Stenotus* Nutt., *Stephanodoria* E. Greene, *Tonestus* A. Nels. (6), *Townsendia* Hook., *Vancleavea* E. Greene, *Xanthisma* DC., *Xanthocephalum* Willd. (5), and *Xylothamia* Nesom *et al.* In these genera, the crystals may be restricted to the corolla tube or they may extend into the throat.

18. The disc corolla lobes are either glabrous, invested with Type C trichomes noncapitate or only slightly capitate, or else they have uniseriate, acicular hairs clearly homologous with Type A trichomes found elsewhere on the plant. The occurrence of the latter on disc corolla lobes is rare in the *Astereae* (Nesom pers. obs.), and this feature probably has had a single origin in the goldenaster lineage, with losses in a number of the taxa; the distribution of character states could with equal parsimony be regarded as a number of parallel gains.

In *Pityopsis*, only *P. falcata* (Pursh) Nutt. and *P. ruthii* (Small) Small have disc corolla lobes with Type A trichomes. Lobes of the other species of *Pityopsis* usually have Type C trichomes or else they are glabrous, although some individuals of *P. microcephala* (Small) Semple produce *Zwillingshaare* on the disc corolla lobes. *Pityopsis falcata* and *P. ruthii* are among the four species hypothesized by Semple & Bowers (1985), apparently based on their geographic distribution, to be the most primitive in the genus. The genus is scored here as primitively possessing Type A trichomes on the disc corollas. Similar variation occurs in *Noticastrum*, where only *N. hatschbachii*, *N. acuminatum* (DC.) Cuatr., and *N. macrocephalum* (Baker) Cuatr. have lobes hairy with Type A trichomes.

19. The vascular traces, usually of 2-4 veins extending to nearly the tip of the style appendages, are densely sclerified in all of the goldenaster genera. Sclerification of such traces is variable in other genera of *Astereae* (Nesom pers. obs.).

20-24. Possible homologies among the different achene morphologies are among the most difficult to interpret. The achenes of *Noticastrum*, *Heterotheca* sect. *Ammodia*, *Tomentaurum*, *Pityopsis*, *Croptilon*, and *Osbertia* produce 6-26 thin, whitish, superficial and slightly raised, evenly spaced nerves; *C. rigidifolium* (Smith) Smith has four resinous, larger nerves interspersed between smaller ones. In cross section, the achenes are fusiform and terete to slightly compressed (in *Pityopsis*, *Osbertia*, and *Croptilon*), but among the goldenasters compressed achenes appear to be primitive. In *Heterotheca* sect. *Ammodia* and *Tomentaurum* the achenes are very strongly compressed; in *Noticastrum* they are plump but distinctly compressed. The ray achenes of *Heterotheca* sect. *Heterotheca* are 3 angled, most in sect. *Phyllotheca* are 2 angled, but those of *H. stenophylla* are slightly but distinctly 3 angled.

In *Heterotheca* sects. *Heterotheca* and *Phyllotheca*, one to several of the facial nerves of the disc achenes are resinous and clearly evident but not raised above the achenial surface. No other achenes of the group are like these, although three specialized species of *Chrysopsis* and one of *Croptilon* produce thick, distinctly raised, resinous veins. The achenes of most *Chrysopsis* (including *Bradburia*) are distinctive in their walls with broad and rounded ridges, the nerves completely below the surface. This feature separates *Chrysopsis* from *Osbertia* and *Noticastrum*, but it is not found in any of the other goldenaster genera. The achenes of *H. oregona*, with numerous superficial nerves, are most like those of *Tomentaurum*, although none of the goldenaster achenes have as many nerves (10-14) as in *H. oregona*. The 2-3(-6) nerved achenes of *Ionactis* are probably themselves evolutionarily derived from immediate ancestors with a greater number of achenial nerves, since these are common among the genera with keeled phyllaries and a base chromosome number of $x = 9$.

Among the taxa of *Heterotheca* sect. *Heterotheca*, achene shape is relatively constant. In *Heterotheca* sect. *Phyllotheca*, the achenes vary from long and nearly straight sided, much like *H. oregona*, to shorter and obovate as in sect. *Heterotheca*. The achenes of *Noticastrum*, while somewhat obovate, are relatively long.

25. In the goldenaster lineage, the pappus typically comprises numerous, basally terete, antrorsely barbellate bristles and an additional, very short, "outer" series of setae, very slender bristles, or linear scales. In *Osbertia* and *Croptilon* there is no outer pappus and the bristles are somewhat reduced in number; in some species of *Chrysopsis* as well as in *Heterotheca* sect. *Ammodia*, the outer pappus is represented only by a few inconspicuous setae. Both *Chrysopsis* and sect. *Ammodia* have been scored as having an outer pappus, and in the phylogenetic hypothesis presented here, its apparent total absence in the other two genera is interpreted as apomorphic. A double pappus also occurs in *Ionactis* and apparently is primitive for the goldenasters as well as related genera (Nesom in prep.).

26. The pappus bristles in most of the goldenasters are terete from base to tip, with the divergent, "ciliate" hairs emerging spirally from all around the bristle. In contrast, the bristles of *Heterotheca* can be seen to be flattened, with the cilia arranged in two lateral rows, even though they are very slender. In some cases, this is most apparent immediately above the bristle base. There is variation among the species of *Ionactis*, but it has been scored as having terete bristles (see comments in Nesom & Leary submitted).

TWO NEW SPECIES OF *ARCHIBACCHARIS* (ASTERACEAE: ASTEREEAE)
FROM MÉXICO WITH A REEVALUATION OF SECTIONAL GROUPINGS IN
THE GENUS

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ABSTRACT

Six sections are recognized within the genus *Archibaccharis*, compared to the two previously recognized by Jackson. The four newly described sections, which are primarily segregated from sect. *Archibaccharis* sensu Jackson, are sect. **Tomentosa**, sect. **Stricta**, sect. **Glandulicarpa**, and sect. **Stylosa**. In this modified view, the difference between "erect" and "scandent" habit is not as absolute as conceived by Jackson, since five of the six sections include species with scandent tendencies. The sectional placement of all 32 species of the genus is proposed, including two species that are described as new. *Archibaccharis tuxtlenensis* sp. nov. (sect. *Glandulicarpa*) is described from the peak of Volcán San Martín Tuxtla in Veracruz, México. *Archibaccharis vesticaulis* sp. nov. (sect. *Stylosa*) from southern Chiapas is apparently most closely related to *A. salmeoides* (S.F. Blake) S.F. Blake.

KEY WORDS: *Archibaccharis*, Asteraceae, Astereae, México, taxonomy

I. Sectional classification of *Archibaccharis*

The taxonomic revision of the genus *Archibaccharis* Heering by J. D. Jackson (1974, 1975) provided a detailed and coherent taxonomic interpretation of the genus, but since his study there have been changes in the nomenclature and delimitation of numerous taxa (Nesom 1988a), and a number of additional species have been described (Turner 1984; Sundberg 1984; Nesom 1988b, 1989, 1990). Jackson divided the genus into two sections, based on the habit of the plants (erect - sect. *Archibaccharis* vs. scandent - sect. *Hirtella* J.D. Jackson). In a reevaluation of the relationships of all the species, the present study divides sect. *Archibaccharis* sensu Jackson into four separate sections, three of

them previously undescribed, and two species of sect. *Hirtella* are transferred to a fourth new section, where they join a third species described in the present paper.

Archibaccharis Heering, Jahr. Hamb. Wissensch. Anst. 21, Beiheft 3:40. 1904.

Type species: *A. hieraciifolia* Heering (= *A. auriculata* [Hemsl.] Nesom)

1. Sect. *Archibaccharis* Type species: *A. auriculata* (Hemsl.) Nesom, *Phytologia* 65:123. 1988.

Plants erect to subscandent, 0.5-2.0(-3.0) m tall, stems greenish, herbaceous, straight to weakly zig-zag, stems and leaves stipitate glandular, eglandular in some, leaves slightly thickened but not coriaceous, capitulescences corymboid and terminal (rounded paniculate and axillary in *Archibaccharis blakeana* Standl. & Steyerf. and *A. pringlei* [Greenm.] S.F. Blake), pistillate heads 6-10(-15) mm high (4-6 mm in *A. pringlei* and *A. blakeana*), on relatively long pedicels, staminate flower styles with linear collecting appendages (0.6-)0.8-1.2 mm long, achenes strigose to glabrous, eglandular.

Species included: *Archibaccharis auriculata*, *A. campii* S.F. Blake, *A. hieracioides* (S.F. Blake) S.F. Blake, *A. macdonaldii* Nesom, *A. simplex* (S.F. Blake) S.F. Blake, *A. blakeana*, and *A. pringlei*.

Only the first two species listed have all of the features noted above, but the section appears to be monophyletic. The first four species produce a stipitate glandular vestiture, and the first five have larger heads than any others in the genus. *Archibaccharis simplex* is distinct in its glabrate, nonglandular vestiture but has an erect habit, sessile to slightly clasping leaves, and produces a corymboid capitulescence of large heads on long pedicels. *Archibaccharis hieracioides* and *A. macdonaldii* have petiolate leaves, but the petioles are broad, and in the latter, they have a flaring, foliar base. Jackson (1975) placed *A. blakeana* and *A. campii* in sect. *Hirtella* because of their subscandent tendencies (he characterized them as "weak-stemmed scramblers"), fractiflex stems, but in their auriculate leaves and linear collecting appendages, they appear to belong in sect. *Archibaccharis*.

2. Sect. *Glandulicarpa* Nesom, *sect. nov.* Type species: *Archibaccharis standleyi* S.F. Blake, *J. Washington Acad. Sci.* 19:271. 1929.

Herbae erectae vel subscandentes, folia plerumque coriacea, appendices styli lineares 0.8-1.0 mm long, achenia glandulosa.

Plants 0.4-3.0 m tall, erect but usually with marked subscandent tendencies (sprawling, leaning, or climbing), stems greenish, herbaceous, straight to weakly zig-zag, glabrous or glabrate (except for *Archibaccharis corymbosa*), leaves thick, lanceolate to ovate, glabrous to glabrate with a shiny upper surface, capitulescence corymboid to rounded or convex paniculate, terminal or

terminal and axillary, pistillate heads 4-7(-8) mm high, on relatively short pedicels, staminate flower styles with linear to linear-lanceolate collecting appendages 0.8-1.0 mm long, achenes glandular and usually strigose as well.

Species included: *Archibaccharis standleyi* (including *A. aequivenia* [S.F. Blake] D. Nash), *A. nicaraguensis* Nesom, *A. venturana* Nesom, *A. tuxtzensis* Nesom, *A. veracruzana* Nesom, *A. subsessilis* S.F. Blake, *A. linearilobis* J.D. Jackson, and *A. corymbosa* (J.D. Smith) S.F. Blake.

Archibaccharis subsessilis, *A. linearilobis*, and *A. corymbosa* produce ovate leaves with truncate to cordate bases and relatively long ligules on the pistillate flowers and appear to form a closely related group; the leaves of the first two are epetiolate or nearly so. *Archibaccharis veracruzana*, *A. venturana*, and *A. tuxtzensis* have ovate leaves with tapering bases, while the rest have lanceolate leaves.

3. Sect. **Stricta** Nesom, *sect. nov.* Type species: *Archibaccharis caloneura* S.F. Blake, Proc. Biol. Soc. Washington 55:117. 1942.

Caules stricti lignescentes porphyreisque et appendices styli lineares 0.8-1.0 mm longi.

Plants 0.6-3.0(-6.5) m tall, strictly erect, stems usually reddish brown, lignescent, straight, glabrous or glabrate, leaves thickened to coriaceous, lanceolate (or ovate to ovate-lanceolate in *Archibaccharis asperifolia*), capitulescence corymbose or broadly paniculate, terminal, rarely also from the upper axils, pistillate heads (3.5-)4.0-7.5(-9.0) mm high, on relatively short pedicels, staminate flower style appendages linear to linear-lanceolate, 0.8-1.0 mm long, achenes sparsely strigose, eglandular.

Species included: *Archibaccharis caloneura*, *A. androgyna* (Brandeg.) S.F. Blake, *A. panamensis* S.F. Blake, *A. irazuensis* (S.F. Blake) S.F. Blake, *A. jacksonii* Sundberg, and *A. asperifolia* (Benth.) S.F. Blake (including *A. sescenticeps* [S.F. Blake] S.F. Blake).

Archibaccharis caloneura and *A. androgyna* have coriaceous leaves and appear to be closely related. *Archibaccharis irazuensis*, *A. panamensis*, and *A. jacksonii* have thinner leaves, and as pointed out by Sundberg (1984), the last two have more achenial nerves than any other species of the genus. *Archibaccharis asperifolia* is unusual in its broader leaves and the strongly developed indument on its leaves, but in diagnostic features it belongs with sect. *Stricta*.

4. Sect. **Tomentosa** Nesom, *sect. nov.* Type species: *Archibaccharis serratifolia* (Kunth) S.F. Blake, Contr. U. S. Natl. Herb. 26:236. 1930.

Herbae erectae vel subscandentes, caules ac folia tomentosa vel villosa, appendices styli deltati vel triangulares 0.2-0.5 mm long.

Plants 0.5-3.0 m tall, erect to leaning or sprawling, stems greenish, herbaceous, straight to weakly zig-zag, stems and leaves sparsely to densely tomentose or villous, the leaves thickened, lanceolate-ovate, capitulescence corymboid or rounded panicle, terminal, sometimes with axillary branches, pistillate heads most 2.0-5.0 mm high, on relatively short pedicels, staminate flower styles with deltate to triangular appendages 0.2-0.5 mm long, achenes sparsely strigose, eglandular.

Species included: *Archibaccharis serratifolia*, *A. nephocephala* Nesom, and *A. peninsularis* S.F. Blake.

These three species are similar in their primarily erect habit, vestiture, and style branch morphology. *Archibaccharis corymbosa* of sect. *Glandulicarpa* also produces tomentose vestiture, but the similarity clearly is parallel. The only other species in which the style collecting appendage are so short are those of sect. *Hirtella*, and the two groups may ultimately prove to be closely related, despite their disparity in habit.

5. Sect. *Stylosa* Nesom, sect. nov. Type species: *Archibaccharis lucentifolia* L.O. Wms., Fieldiana, Bot. 29:388. 1962.

Herbae scandentes vel subscandentes, appendices styli ovati-deltati 0.7-0.8 mm long.

Plants subscandent herbs (up to 5 m tall) or true vines, stems greenish, herbaceous, straight to weakly zig-zag, stems and leaves glabrous to glabrate, the leaves coriaceous to slightly thickened, ovate, capitulescence rounded panicle, terminal and axillary, pistillate heads 3.0-8.0 mm high, on relatively short pedicels, staminate flower styles with ovate-deltate appendages 0.7-0.8 mm long, achenes sparsely strigose, eglandular.

Species included: *Archibaccharis lucentifolia*, *A. salmeoides* (S.F. Blake) S.F. Blake, and *A. vesticaulis* Nesom.

These species are separated primarily on the basis of their very thick staminate style branch appendages with thick, spreading, sweeping hairs. No other species of the genus are similar. The first two species are strongly scandent, while *Archibaccharis vesticaulis* is more shrublike. All have thick leaves, and their relationship may prove to be with sect. *Glandulicarpa*, where their position would be analogous to the two of sect. *Archibaccharis* that are hypothesized to have evolved a scandent habit from primarily erect ancestors.

6. Sect. *Hirtella* J.D. Jackson, Phytologia 32:158. 1975. Type species: *Archibaccharis hirtella* (DC.) Heering, Jahr. Hamb. Wissensch. Anst. 21, Beiheft 3:41. 1904.

Scandent herbs, sometimes leaning, stems greenish, sharply zig-zag to sinuous, stems and leaves hirsute to sparsely hirsutulous, the leaves thin and not

shiny, ovate, capitulescence mostly rounded to convex panicles, terminal and axillary, heads 3.5-5.5(-7.0) mm high, on relatively short pedicels, of the staminate flower styles with minute, ovate-deltate collecting appendages 0.2-0.5 mm long, achenes strigose, eglandular.

Species included: *Archibaccharis hirtella**, *A. intermedia** (S.F. Blake) B. Turner, *A. albescens** (J.D. Jackson) Nesom, *A. taeniotricha** (S.F. Blake) Nesom, *A. flexilis* (S.F. Blake) S.F. Blake, and *A. schiedeana* (Benth.) J.D. Jackson.

From sect. *Hirtella* as delimited by Jackson (1975), *Archibaccharis salmeoides* and *A. lucentifolia* have been transferred to sect. *Stylosa*, and *A. pringlei* and *A. blakeana* have been transferred to sect. *Archibaccharis* sensu stricto.

Jackson (1975) pointed out the similarity in collecting appendages among the taxa he regarded as four varieties of *Archibaccharis hirtella* (marked with asterisk above). These are the core of sect. *Hirtella* and are here considered four separate species. *Archibaccharis flexilis* shares with *A. taeniotricha* and *A. albescens* a truly scandent habit and densely hispid stems with coarse, erect, long, sharp pointed trichomes. The collecting appendages of both *A. flexilis* and *A. schiedeana*, however, are much more linear than the core species, and the evolutionary affinities of both of these may ultimately prove to belong elsewhere.

As noted by Jackson (1975), the plants of *Archibaccharis schiedeana* are initially decumbent or procumbent to sprawling or arching herbs, but at maturity the stems elongate greatly and they become true vines. Plants of *A. hirtella* and its three closest relatives, however, as well as *A. flexilis*, have been collected only as vines. The stems of most of the scandent plants are zig-zag ("fractiflex" in the terminology of Jackson 1975) and produce a terminal capitulescence as well as similar sized axillary ones at least on the upper portions, while those of erect plants are usually relatively straight and produce only a single, terminal capitulescence. The stems of many of the erect species in other sections with scandent tendencies, however, tend to be slightly zig-zag, and the capitulescences are often axillary as well as terminal. Further, the stems even of the scandent species are variable in orientation. For example, the stems of *A. schiedeana* are usually nearly straight, and *A. flexilis* has sinuous rather than zig-zag stems. In any case, the definite and consistent tendency for plants of almost all species of *Archibaccharis* to become at least somewhat vinelike argues for the monophyletic status of the genus. It is assumed, however, that primarily erect stems, rather than true vines, are the primitive condition for the genus.

II. Two new species

Continued study of *Archibaccharis* has revealed the existence of two previously undescribed species. The first apparently is restricted to Veracruz,

México, where it is known only from Volcán San Martín Tuxtla.

Archibaccharis tuxtlensis Nesom, *sp. nov.* TYPE: MÉXICO. Veracruz: Mpio. San Andres Tuxtla, near summit (upper 300 ft) of Volcán San Martín, ca. 6000 ft, 28 Dec 1964, *A.C. Faberge s.n.* (HOLOTYPE: TEX!).

Differt a *A. venturana* Nesom phyllariis interioribus longioribus, corollis staminalibus longioribus, et acheniis glandes non nisi ferentibus.

Subscandent shrubs ca. 0.5 m tall, stems noticeably but not strongly zigzag, eglandular, sparsely to moderately invested with thick, vitreous hairs with conspicuous brownish crosswalls. Leaves thick, the upper surface shiny, with a raised reticulum of veins, mostly glabrous except along the midvein, lower surface with a duller texture, blades ovate with acuminate apices and rounded to obtuse bases, 5-10 cm long, 2-4 cm wide, on petioles 5-8 mm long, the margins minutely and widely mucronulate with 2-9 pairs of mucros. Capitulescences axillary and terminal on the upper portion of the stems, in rounded, ebracteate panicles. Staminate heads not seen. Pistillate heads with 7-12 outer, pistillate flowers and 1 central, staminate flower; phyllaries lanceolate, greenish, with fringed-ciliate distal margins, otherwise glabrous, in 3-4 graduated series, the inner 4.5-5.5 mm long, the outer 1/5 as long. Pistillate flowers fertile, the corollas eligulate or with an extension 0.2 mm long, the tube 2.5-3.5 mm long, with thick, viscid trichomes, the style 2.5-3.5 mm long, with branches 1 mm long; achenes 1.2-1.5 mm long, gland dotted and viscid, without other hairs; pappus of numerous bristles. Staminate flowers with sterile ovaries, the corollas 3.5-4.0 mm long, the lobes purplish, lanceolate, 1.5 mm long, cut 2/3 to the tube, tube densely hairy with viscid trichomes.

Additional collection examined: MÉXICO. Veracruz: Mpio. San Andres Tuxtla, top of Volcán San Martín Tuxtla, ca. 1730 m, 14 Feb 1972, *Beaman & Castillo 5686* (TEX).

Archibaccharis tuxtlensis is most similar in habit, leaf morphology, and fruit morphology to *A. venturana* and *A. subsessilis* of sect. *Glandulicarpa*. The new species is distinguished from its closest relatives by the following contrasts.

1. Leaves gland dotted above and beneath, not distinctly thick or shiny, basally rounded to slightly cordate, sessile or on petioles 1 mm long; heads mostly in loose, broad, terminal corymbs; pistillate corollas eligulate; Guatemala, Chiapas, and Oaxaca. *A. subsessilis*
1. Leaves eglandular, thick, the upper surface shiny, basally obtuse to acute, on petioles 5-8 mm long; heads in relatively dense, terminal and axillary, corymboid panicles; pistillate corollas eligulate or essentially so; Veracruz. (2)

2. Inner phyllaries 2.0-3.0 mm long; pistillate heads with 2 staminate flowers, the corollas 2.0-2.8 mm long; achenes both sparsely strigose and glandular; vicinity of Xalapa to Perote. *A. venturana*
2. Inner phyllaries 4.5-5.5 mm long; pistillate heads with 1 staminate flower, the corolla 3.5-4.0 mm long; achenes glandular, without other vestiture; Volcán San Martín Tuxtla. *A. tuxtensis*

Archibaccharis vesticaulis Nesom, sp. nov. TYPE: MÉXICO. Chiapas: Mpio. Las Margaritas, E of Comitán Dominguez, 2.5 mi E of Ejido Tziscaco turnoff, along a short spur road toward lake, disturbed ground, 7 Jan 1984, S. Sundberg 2423 (HOLOTYPE: TEX!).

Differt a *A. salmeoide* (S.F. Blake) S.F. Blake habitu subscandenti, foliis glandulosis, caulibus dense pubescentibus, capitulis brevioribus, et corollis staminalibus brevioribus.

Subscandent shrubs 5 m tall, stems slightly zig-zag, invested with thick, reddish brown trichomes completely obscuring the stem surface, eglandular. Leaves coriaceous, dark green, the upper surface shiny, with a slightly raised reticulum of veins, sparsely and minutely puberulous along the veins, eglandular, lower surface minutely but definitely gland-dotted, the blades elliptic-obovate with short attenuate apices and acute bases, 3-9 cm long, 2-4 cm wide, on petioles 5-15 mm long minutely but densely viscid puberulous, the margins entire or usually mucronulate with 2-7 pairs of mucros. Capitulescence of rounded, ebracteate panicles, terminal and on short axillary branches. Staminate heads not seen. Pistillate heads with 11-12 outer, pistillate flowers and 1 central, staminate flower; phyllaries narrowly oblong-lanceolate, greenish, with fringed ciliate distal margins, otherwise glabrous, in 3-4 graduated series, the inner 3.0-4.0 mm long, the outer 1/5 as long. Pistillate flowers fertile, the corollas tubular-filiform, 2.0-2.4 mm long, with a purple apex, eligulate; achenes 1.2-1.4 mm long, flattened, with 3-4 thick nerves, sparsely strigose, eglandular; pappus of numerous bristles. Staminate flowers with sterile ovaries, the corollas 3.0-3.2 mm long, the tube 1.8-2.0 mm long, densely hairy with viscid trichomes, the lobes purple, lanceolate, 1.2 mm long, cut nearly to the tube, style branches 0.8 mm long, with broad, elliptic-ovate appendages 0.5 mm long.

Additional collection examined: MÉXICO. Chiapas: Mt. Pasitar, Jan 1937, *Matuda 1544* (MEXU).

Jackson (1975) cited a MICH duplicate of *Matuda 1544* as a specimen of *Archibaccharis schiedeana*, but the MEXU specimen is clearly the same as the type. *Archibaccharis schiedeana* has neither coriaceous leaves nor densely invested stems, and its style branch morphology is very different from that of *A. vesticaulis*. The new species appears to be most closely related to *A.*

salmeoides and *A. lucentifolia* and is placed with them in sect. *Stylosa*. It is distinguished from *A. salmeoides* by the following contrasts.

1. Stems densely invested with reddish brown trichomes, obscuring the surface; lower surface of leaves sessile-glandular; pistillate heads 3.0-4.0 mm high; staminate corollas 3.0-3.2 mm long. *A. vesticaulis*
1. Stems sparsely puberulous with relatively thin trichomes; leaves eglandular; pistillate heads 4.0-6.4 mm high; staminate corollas 3.9-4.4 mm long. *A. salmeoides*

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SARCOSTEMMA CLAUSUM, SERIES *CLAUSA* (ASCLEPIADACEAE),
NEW TO TEXAS

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ABSTRACT

Sarcostemma clausum (Jacq.) Roemer & Schultes, subgenus *Ceramanthus*, series *Clausa* (Asclepiadaceae) previously unreported in Texas has been found in Hidalgo County. A key is provided for the Texas species of *Sarcostemma*.

KEY WORDS: *Sarcostemma*, *Sarcostemma clausum*, subgenus *Ceramanthus*, series *Clausa*, Asclepiadaceae, Texas

Sarcostemma clausum (Jacq.) Roemer & Schultes, subgenus *Ceramanthus* Kunze, series *Clausa* Holm (Asclepiadaceae) was first described by Jacquin (1763) as *Cynanchum clausum*. Roemer & Schultes (1820) moved it to *Sarcostemma*. *Sarcostemma clausum* is a southern species, reported from southern Florida, México (including Baja California Sur), Central America, South America, and the Caribbean Islands (Holm 1950). Members of this genus are twining or trailing vines which climb by turning to the right. They have milky sap; conspicuous flowers with a 5 lobed calyx, corolla rotate to almost campanulate, 5 lobed, and 5 filaments forming a column. The fruits are follicles, fusiform or obclavate in shape.

Cory & Parks (1937), Holm (1950), Correll & Johnston (1970), Gould (1975), nor Hatch *et al.* (1990) listed *Sarcostemma clausum* as occurring in Texas. Based on previously mapped distributions (Holm 1950), it appears that *S. clausum* has had a natural migration up the eastern coastline of México from the state of Tamaulipas to its present location in Hidalgo Co., Texas. There are now four (4) species of *Sarcostemma* with five (5) taxa represented in Texas.

The following key; modified from Correll & Johnston (1970), will differentiate the *Sarcostemma* found in Texas.

KEY TO TEXAS *SARCOSTEMMA*

1. Peduncles as thick as, or thicker than the adjacent internode.
 *Sarcostemma clausum* (Jacq.) Roemer & Schultes
- 1' Peduncles thinner than the adjacent internode.
 2. Margins of leaves crisped, occasionally purple tinged, sepals mostly greater than 3 times as long as wide. *S. crispum* Benth.
 - 2' Margins of leaves not crisped, green, sepals mostly less than 3 times as long as wide.
 3. Sepals 4-6 mm long, pubescent on both surfaces.
 *S. torreyi* (A. Gray) Woodson
 - 3' Sepals 2-3 mm long, pubescent on back side (dorsal) only.
 4. Blades cordate at base, mostly less than 3 times as long as wide. *S. cynanchoides* Dcne. var. *cynanchoides*
 - 4' Blades hastate to rounded cuneate at base, greater than 3 times as long as wide.
 *S. cynanchoides* var. *hartwegii* (Vail) Shinners

Specimen collected: UNITED STATES. Texas: Hidalgo Co., west side of the westernmost resaca in Bentsen-Rio Grande Valley State Park, south of Mission, 27 Dec 1988, *S. & G. Jones 2229* (TAES). It was frequent, climbing on *Celtis* along the wooded resaca adjacent to an open fallow field. Associated genera: *Celtis*, *Salix*, *Pennisetum*, and *Phragmites*. The soils are of the Rio Grande-Matamoros association (RT) and are deep, moderately and slowly permeable, loamy soils of floodplains and low terraces. More specifically they are typically light brownish gray or grayish brown silt loam or have a silty clay surface layer. The geology of the site is of Alluvium formation (Qos) (Recent).

During follow up trips in December 1989 and 1990, vines of *Sarcostemma clausum* were found, but in neither year did we find it in flower.

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BOOKS RECEIVED

Memoria II Simposio Latinoamericano de Briologia. Claudio Delgadillo M. (ed.). Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F. México. 1991. 48 pp. Price unknown. No ISBN.

The book comprises papers from a symposium on bryophytes held in conjunction with the fifth Latin American botanical Congress which was held in Havana, Cuba in June 1990. Eight papers are included, authored by nine individuals. Most of the presentations deal with mosses or liverworts of Cuba. One paper treats Frullaniaceae in Brasil, and another examines distribution patterns of neotropical mosses.

Phytochemical Induction by Herbivores. Douglas W. Tallamy & Michael J. Raupp (eds.). John Wiley & Sons, Inc., 1 Wiley Dr., Somerset, New Jersey 08875-1272. 1991. 431 pp. xx. \$98.00 (hardcover). ISBN 0471-63241-4.

A total of 33 contributors participated in writing this book. As stressed by the editors in their preface, the concept of phytochemical induction in response to herbivory is extremely difficult to study and quantify. Authors of papers in the present volume have examined a number of different plant taxa (aspen, birch, gourds, grasses, tobacco, etc.) subjected to several different types of actual or simulated herbivore stress. Plant responses have been measured by examination of a number of different plant products from alkaloids to phenolics. Effects of plant response on the herbivores was also examined. Most of the papers are of a review nature. The book as a whole provides a broad spectrum of activity in this field.

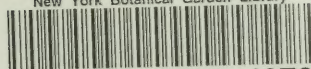
Plant Genetic Resources of Ethiopia. J.M.M. Engels, J.G. Hawkes, & Melaku Worede (eds.). Cambridge University Press, 40 W. 20th St., New York, New York 10011. 1991. 383 pp. xv. \$85.00 (hardcover). ISBN 0-521-38456-7.

The plant genetic resources of Ethiopia are described by a total of 29 contributors to thirty papers in this book. The contributors are participants in an Ethiopian Plant Genetic Resources Center, and are familiar with the genetic resources of Ethiopia and how they may relate to similar resources in other parts of the world. Four sections in the book give a general introduction, describe Ethiopia as a center of plant genetic diversity, describe germplasm collection and conservation efforts in Ethiopia, and describe methods of evaluation and utilization of Ethiopian plant genetic resources.

Vascular Plants of Minnesota A Checklist and Atlas. Gerald B. Ownbey & Thomas Morley. University of Minnesota Press, 2037 University Avenue SE, Minneapolis, Minnesota 55414. 1991. 307 pp. xi. \$39.95 (cloth with dust jacket). ISBN 0-8166-1915-8.

The introduction to this work provides a brief but useful history of botanical activity in Minnesota, with references to previous floristic works. Also included in the preface material is a vegetation map for the state. The bulk of the work consists of two parts. First, the checklist (by Ownbey), wherein each plant known to occur in the state is listed along with synonyms (those used in past treatments for the state). Families and genera are listed alphabetically within the major categories of Pteridophytes, Gymnosperms, and Angiosperms. Each genus citation is accompanied by a reference to the maps in the atlas where distributions for the included species may be found, and for most, references to recent studies of the genus. The atlas (by Morley) follows the same order as the checklist. Localities for each species are reported on individual maps showing the outlines of counties in the state. Dots representing localities are placed so as to reasonably accurately reflect the localities, not merely to indicate the presence of the plant in a given county. Thus, multiple localities may be indicated in a single county for any given species.

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